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REVISION OF THE GENUS PETALOSTEMON (LEGUMINOSAE)[1]

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ABSTRACT. This paper is a taxonomic revision of the genus Petalostemon (Leguminosae). The validity and delimitation of Petalostemon, especially the relationships with Dalea are considered. On the basis of evidence from cytology, floral morphology and vascular anatomy, Petalostemon is defined as a taxon of perennial plants allied to, but distinct from Dalea.

Twenty-nine species and two subspecies are recognized within the two subgenera of Petalostemon. Investigations of the putative taxa were based primarily upon field collections and observations, greenhouse culture, compatibility investigations, cytology, pollen analysis and herbarium studies. Mass collection analyses were used to verify suspected hybridization among certain of the species in field populations; but hybridization was a relatively rare event in the genus. Cytological studies verified a gametic chromosome number of $n = 7$; determinations are presented for 9 species heretofore unreported. One new species is characterized.

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INTRODUCTION

Petalostemon, as herein delimited, comprises 29 species of North American papilionoid legumes of the tribe Psoraleae (Rydberg 1928a, b; Isely 1958, 1962; Lersten and Wemple 1966).

The most recent worldwide treatment of the Leguminosae (Hutchinson 1964) divides the Psoraleae into two tribes, Daleae and Psoraleae. Petalostemon and its close relative Dalea are placed in the former tribe. Evidence contrary to Hutchinson's division is presented by Lersten and Wemple (1966).

The genus is distinguished from other members of the tribe by the possession of both of two basic characters: 1) there are only five stamens and 2) the four petals other than the standard are inserted at the apex of

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the staminal tube and alternate with the filaments, while the standard is inserted at the floral base.

The original objective of this investigation was the delimitation of the taxa within Petalostemon. It soon became evident, however, that a reconsideration of the generic limits of Petalostemon was desirable, if not essential. A considerable proportion of the total research, therefore, was directed toward the latter end, particularly the interrelationships of Petalostemon and Dalea. Much of this material is in print (Wemple and Lersten 1966) and will only be summarized in this paper.

MATERIALS AND METHODS

Field collections and observations

Field studies of Petalostemon were conducted during the growing seasons 1961-1964 inclusive. All species of the genus were studied in situ except those few indigenous to the Great Basin and the Pacific Northwest. Living material was also collected and placed under greenhouse conditions for additional study.

Greenhouse cultivation

Plants were grown from both rootstocks and seeds. Rootstocks collected in the field were transported to the greenhouse in polyethylene bags. The potting medium was Iowa prairie soil with approximately 25% coarse river sand added to facilitate drainage.

Following threshing and scarification, seeds were germinated on moistened blotter paper in Petri dishes placed in a 20°C constant temperature chamber in the Iowa State University Seed Laboratory. When seedlings were 1—cm long, they were transferred to pots containing the medium. Voucher specimens of all plants cultured were deposited in ISC.

Hybridization studies

A program of controlled cross pollinations in the greenhouse was initiated in an attempt to elucidate genetic relationships within the genus. Since most species of Petalostemon are obligately entomophilous, there is no self fertilization in an insect free greenhouse; therefore, the common practices of "bagging" and emasculation are unnecessary. Pollination was carried out by using a stamen as a pollen applicator—merely touching it to the stigmas of the female parent. Complete pollination of a spike usually took about 2 weeks because the flowers open sequentially.

In the field, fruits are presumably shaken from the rachis by wind and rain action. Lacking this dispersal force in the greenhouse, the fruits remain attached to the rachis and can conveniently be collected when the seeds of a whole spike mature.

Cytological studies and pollen analysis

Cytological material was obtained in part from germinated seeds. Root tips were cut off when they attained a length of 1—2 cm and immediately placed in a one-fourth strength nutrient solution (Hoagland and Arnon 1950) with 0.02% Acti-dione (Upjohn Co.), a mitotic inhibitor. After 7—8 hours treatment, they were fixed in 3:1 alcohol-acetic acid for 24 hours. The root tips were then hydrolyzed for 8—9 minutes in 1N HCl at 60°C and placed in Feulgen stain for 45—70 minutes. Following "squashing," the slides were made permanent by the liquid CO_2 freezing technique (Bowen 1956).

Meiotic counts were obtained from buds collected in the field as well as the greenhouse. Fixation was by 3:1 alcohol-acetic acid, and the preferred stain was propiocarmine. All cytological illustrations were made using the Zeiss Drawing Attachment. Voucher specimens of all plants from which successful counts were obtained were deposited in ISC.

Pollen was collected from living plants, both in the field and the greenhouse, as well as from herbarium specimens. Semipermanent slides were prepared by using lactophenol-cotton blue (Sass 1958; Stone 1963) as a combination stain and mounting medium. Fresh pollen can be studied within a few hours; samples from herbarium specimens require 24 hours to allow the stain to penetrate and inflate the dehydrated grains. Length, width and stainability were recorded. Stainability is an approximation of viability.

Herbarium Study

Over 4,000 herbarium specimens were studied during this investigation. I should like to express my appreciation to the curators of the following institutions who made them available. Those herbaria denoted by an asterisk supplied type material only. Abbreviations used for all herbaria cited in this paper are those of Lanjouw and Stafleu (1964).

*B	Botanisches Museum
D	Duke University
*F	Chicago Natural History Museum
FLAS	University of Florida
FSU	Florida State University
*G	Conservatoire et Jardin botaniques
GA	University of Georgia
*GH	Gray Herbarium of Harvard University
*GL	University of Glasgow
ISC	Iowa State University
*KANU	University of Kansas
KY	University of Kentucky
MO	Missouri Botanical Garden
NO	Tulane University
NY	New York Botanical Garden
OKLA	Oklahoma State University
*P	Muséum National d'Histoire Naturelle Laboratoire de Phanérogamie
*PH	Philadelphia Academy of Natural Sciences
RM	Rocky Mountain Herbarium
SMU	Southern Methodist University
TENN	University of Tennessee
TEX	University of Texas
*UC	University of California, Berkeley
US	United States National Herbarium
*WS	Washington State University

Synonyms for each species are listed in the taxonomic treatment. The procedure of Isely (1962) is used to indicate the basis for inclusion of each name as follows:

(1) Type specimen of photograph of same examined.

(2) Original description examined.
(3) Name utilization follows that of another author who has examined an original specimen or type.
(4) Name utilization follows that currently accepted; typification not verified.

Multiple designations [e.g., (1)(2)] indicate congruity between the sources of information indicated. The appropriate number(s) follows the citation of each name.

The distributional maps are based on specimens studied by me. A list of cited specimens can be found in my thesis (Wemple 1965).

Clearing techniques

The vascular anatomy of the flowers of Petalostemon and related genera was studied by clearings (Brady, Wemple and Lersten 1964). Herbarium specimens were the major source of material, supplemented by fresh flowers killed and fixed in FAA or GRAF III (Sass 1958). They were cleared in 5% NaOH and chloral hydrate, stained with safranin and mounted in Piccolyte. Clearing without staining by using Hoyer's solution (Anderson 1954) was found a valuable and timesaving technique. Permanent slides were made directly from dissected specimens, softened in a wetting agent (Pohl 1954) and, without resorting to tedious dehydration, mounted in Hoyerls solution.

Certain aspects of anatomy not clearly observable by clearing techniques were studied by microtome sections. These were prepared and stained by conventional methods (Sass 1958).

DELIMITATION AND VALIDITY OF PETALOSTEMON

Petalostemon can usually be distinguished from the closely related genus Dalea by two basic characters: 1) there are only five stamens and 2) the four petals other than the standard are inserted at the apex of the staminal tube alternating with the filaments. Most species of Dalea have nine or ten stamens and nearly all have a distinctly papilionoid corolla. In some species all five petals are inserted on the hypanthium below the staminal tube. More commonly the wing and keel petals are attached at some point on the staminal tube. In others, however, the four anterior petals are inserted almost at the apex of the staminal tube, approximating, but not quite attaining, the Petalostemon condition. This is found in Rydberg's segregate genus Thornbera (Rydberg 1919-1920), a part of Dalea in the broad sense. In gross appearance certain species of Dalea and Petalostemon are easily confused, but inspection of the flowers regarding the just mentioned characters will readily place the specimen in the proper genus.

The question of whether the petals are true petals or staminodes has been a critical one in understanding the relationship between Dalea and Petalostemon. A reappraisal of certain aspects of floral morphology of Petalostemon was undertaken with special regard to the questions of petal origin, petal insertion and stamen number. A detailed account of this work is in print (Wemple and Lersten 1966), and the following is the conclusion of that paper:

There is apparently no clearly defined disjunction between Petalostemon and Dalea, and evidence from vegetative anatomy and floral morphology indicate a common ancestry. A chromosome number of n = 7 is shared by both genera, also indicative of a close relationship. Notwithstanding the similarities between the two genera, Petalostemon represents a highly specialized branch within the heterogeneous daleoid complex. This specialization has resulted in both the loss of one whorl of stamens and the migration of four petals to the apex of the staminal tube. The species of Dalea possessing petalostemoid characteristics appear to arise from diverse sections of the genus and perhaps represent specialized and independent, albeit somewhat convergent evolutionary trends. A complete reassessment of the placement of Petalostemon must await revision of the remainder of the daleoid complex, but it is feasible at present to redefine the generic delimitations of Petalostemon excluding all taxa possessing more than five stamens as well as those with petal insertions substantially below the apex of the staminal tube.

The reticulate, often convergent, pathways taken by the evolutionary processes in many groups often make generic lines somewhat indistinct. This is certainly true in many groups of legumes and emphatically true in other plant families (e.g., Cruciferae, Gramineae). Therefore, at least more than one viewpoint of what constitutes generic delimitation in a particular taxon is admissible. The alternative to the present disposition of Petalostemon, as advocated by Shinners (1949a) and Barneby (1965) would be to reduce it to some subgeneric ranking within Dalea; but again, the same problems would be encountered only at a different taxonomic level. The acceptance of Petalostemon, as herein defined, seems to result in a reasonably natural genus of perennials, easily definable from the melange that is Dalea.

DELIMITATION OF SUBGENERIC TAXA

Two major lines are evident within my delimitation of the genus Petalostemon; subgenus Kuhnistera and subgenus Petalostemon. The first is represented by the specimen originally collected by Walter and herein called P. pinnatum. Michaux (1803), or L. C. Richard who wrote Michaux' diagnoses, was the first to unify Kuhnistera with what were considered the pentastaminate members of Dalea in the new genus Petalostemon, a position with which I concur. Rydberg, in the most recent revision of the Psoraleae (1919-1920), considered the differences sufficient to merit generic status. The basic characteristics used to substantiate separation of the Kuhnistera are: 1) spikes disposed in a corymbose manner; 2) sterile involucral bracts subtending individual spikes; and 3) plumose, filiform calyx lobes. I consider the three taxa composing Kuhnistera to belong within the genus Petalostemon because all the primary identifying characters of this genus are found, in addition to these specialized characterstics that seem merely exaggerations of those found in other species of Petalostemon. For example, Petalostemon multiflorum possesses an inflorescence with a somewhat corymbose structure. Sterile bracts subtending flower spikes are present in all the southeastern species of Petalostemon as well as many other species throughout the range of the genus. None, however, exhibit the degree of

bract expansion found in P. pinnatum. An approach to the plumose-filiform lobes of P. pinnatum is found in P. ornatum of the Pacific Northwest. In short, the features characteristic of subgenus Kuhnistera are quantitatively, but not qualitatively, different from those of other species of the genus. With these considerations in mind, I have adopted Candolle's (1825) viewpoint: one genus, Petalostemon, with two subgeneric categories.

Within subgenus Petalostemon certain groupings can be made based on morphological similarities. I have recognized these groups by using Rydberg's (1919-1920) technique of unofficial sectional names. It is clear from my work that at least some of these sections are more than mere phenotypic associations. The Purpurei, for example, are almost completely interfertile, whereas hybridization between one of its members and another species outside the section is rare. The same is true of the Candidi. Although compatibility studies did not cover all species and sections, it seems clear that morphologically based relationships have a sound genetic basis within this genus.

COMPATIBILITY STUDIES

During the fall of 1962, a program of controlled cross pollinations was begun in an attempt to elucidate the genetic relationships between the species of Petalostemon. Parent plants representing 11 of the 29 species were grown either from seed or field-collected rootstocks and maintained under greenhouse conditions during the experiment. Cross pollinations were made, the seeds harvested, counted, planted, and progeny grown. In a few instances, second-generation hybrids were produced. In addition to the insights into the genetic relationships of the species, this part of the research provided an almost constant supply of cytological material, flowers and pollen for further investigation.

Petalostemon proved an ideal subject for this type of biosystematic research because the plants rarely set seeds if kept in an insect-free environment. The mechanisms preventing self-pollination are not primarily genetic; rather, they are morphological. Almost all species are protandrous, the anthers are exserted and the pollen exposed before stigmatic receptiveness. Additionally, the filaments diverge from the longitudinal axis of the flower so that the anthers are spatially quite remote from the stigma when it does become receptive. Another factor involved is that the style is long and the stigma extends well beyond the anthers. One species that lacks both divergent filaments as well as an elongate style is P. obovatum. This species is entirely self pollinating in the greenhouse, setting seeds readily without outside intervention.

The degree of interfertility between species was measured by the percentage of seeds set in a given cross. Usually all the pods of a particular spike were examined. This number ranged from a minimum of 20 to a maximum of 261. The average number of pods examined from each cross was 32. The results of all attempted cross pollinations are shown in Table 1. A seed set of less than 10% is interpreted as indicating complete intersterility. This small percentage appears to represent infrequent self-pollinations, often resulting from stylar bending that allows a stigma of one flower to touch an anther of a contiguous one.

Table 1. Results of attempted cross-pollinations in the genus Petalostemon, All numbers are expressed in percentage of seed set. The asterisk(*) signifies a self-pollination or progeny phenotypically like the female parent.

Male parents	Female parents (A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	(I)	(J)	(K)
P. purpureum (A)	15 24 48 24 34 61	45 30	0	8 0	2 0 30 12	10	10* 0 5* 3.5*	0 0	--	0 2.4*	--
P. tenuifolium (B)	16 0 9.6 7.8	55 34 45	--	2.4	4 12 4 17	22	12*	0 13* 67* 0 26*	—	0	0
P. tenue (C)	31 53 2.5 0 19	37 0	--	19 9	21 6 16 10 20	--	0	--	0	3.8*	--
P. pulcherrimum (D)	21 4 45 50	10	0	1	3 17	--	0 21*	0 0	--	2.6*	0 0
P. arenicola (E)	41 36 58	45 19 57 14 25	0 0	0 7 8 11 13	53 27	0 0 43	34*	0	0 0	0 0	0
P. gattingeri (F)	53	23	--	0	37 45	--	--	--	—	0	--
P. candidum (G)	0 0 2.3*	0 0	--	--	0	--	--	10 61 11	31	0 0	2* 0
P. occidentale (H)	—	9.1* 0 6.7*	--	--	5.6* 0 0	--	10 50 35	27	28 29	12*	0 0 1.3*
P. multiflorum (I)	--	--	--	--	--	--	--	--	--	--	--
P. villosum (J)	4.3* 0	0 0	--	0 0	12.5* 0 0	--	0	34* 20*	0 0	46	12* 0 0
P. microphyllum (K)	0 1.8 0 0	0 0	0	0 0	0	--	2.8* 30* 0	0 7.5* 0 0 0 0	0	0 0	4.7

In Table 1, the species are arranged according to sectional groupings based on morphological similarities. It will be seen that within a given section, fertility between the species is high, while between sections it is quite low, if existent at all. As a result of progeny analysis, only one intersectional hybrid was verified, that from a cross between P. candidum and P. tenuifolium, with the former the pistillate parent. P. candidum is white flowered while P. tenuifolium is purple. The hybrid was intermediate in color as well as other characteristics. A possible second intersectional cross indicated in Fig. 1 by the question mark is based on rather indirect evidence. The cross was between P. villosum and P. occidentale, the former the pistillate parent. The progeny, phenotypically, was like P. villosum, but most of the flowers were abnormal. Many lacked corolla segments and(or) stamens, others showed various kinds of androecial fusions. These abnormalities could have been the result of self-pollination resulting in increased homozygosity of deleterious recessive genes; however, no other P. villosum crosses showed such abnormalities, including several self crosses.

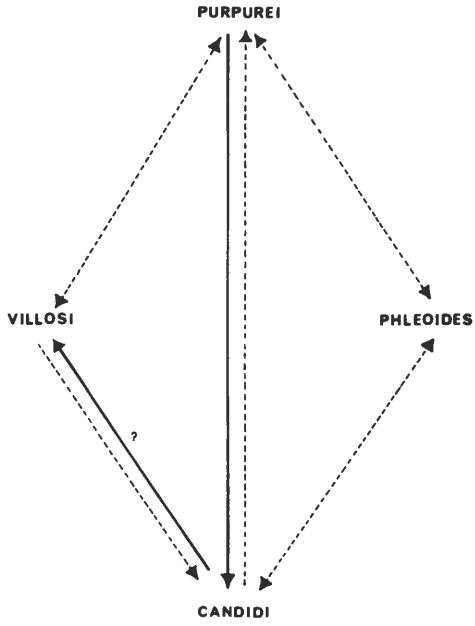


Figure 1. Diagram showing attempted crosses between members of four sections of Petalostemon. The arrows indicate the direction of pollen transfer. Attempted crosses where less than 5% seed set resulted are indicated by a broken line. The solid lines indicate verified hybrids were produced.

Within sections, all crosses showed phenotypic intermediacy between both parents with but a few exceptions. One of the exceptions was the unique retrorse calyx pubescence characteristic of P. tenue (P. stanfieldii). Of the progeny examined when this species was the staminate parent, none had retrorse calyx pubescence even though intermediacy was seen in all other characteristics. It is possible that this character is controlled by a single recessive gene.

One of the anticipated results of these crosses was the synthesis of plants morphologically similar to preexisting species of Petalostemon. A cross between P. gattingeri and P. purpureum resulted in such a synthesis. The progeny of this cross were phenotypically identical with P. arenicola. Although the present range of the two parents is allopatric, it is possible that sympatry existed in the past and that hybrid populations proved adapted to a particular "ecological niche" and persisted. Phenotypic resemblance, however, is equivocal and need not imply the derivation of an entire species from two extant species. A specimen of this cross is in ISC.

Another result of this study was the discovery that male sterility within populations is a relatively common phenomenon in Petalostemon. This is not an artifact of greenhouse culture. It first came to my attention in the greenhouse when certain plants of P. purpureum, P. candidum, and P. multiflorum consistently produced flowers with shrunken anthers containing no pollen yet appeared fully female fertile and set seeds when pollinated with pollen from other plants. Later, close observation in the field showed that, indeed, the field populations contained both male sterile and male fertile plants. On a prairie remnant adjacent to the Ames High School, Story Co., Iowa, both P. purpureum and P. candidum grow sympatrically. Ten of 12 P. purpureum and 27 of 35 P. candidum plants collected here were male sterile.

The obvious advantage of male sterile plants in pollination experiments is that the possibility of accidental self-pollination is eliminated. All three male sterile species in cultivation have thus yielded unequivocal data in this study. One aspect of this male sterility phenomenon is that the progeny of these plants resulting from hybridization with another species in the same section are always male sterile even though they are intermediate in all other phenotypic aspects. This characteristic is possibly the result of one or a group of dominant genes.

Some evidence has accumulated from the studies involving these male sterile plants indicating that "foreign" pollen can induce parthenogenetic seed formation. Crosses involving male sterile P. candidum plants and some of the purple species (e.g., P. purpureum, P. tenuifolium, P. pulcherrimum and P. arenicola) produced relatively high seed set, yet the progeny were phenotypically like the pistillate parent. It is probable that embryo development is parthenogenetic and the foreign pollen merely acts as a trigger for this type of reproduction. Although all the specimens of P. occidentale used were fully male fertile, perhaps parthenogenetic seed formation was responsible for the high seed set with pollen from P. tenuifolium and P. villosum (Table 1). In this instance, too, all the progeny were phenotypically P. occidentale.

In summary, there are genetic barriers between the sections of the genus. Thus two species belonging to different sections can exist sym-

patrically with little, if any, genetic interchange. Within sections, however, interfertility is common, but geographical or ecological separation of species is almost always found. If two species belonging to the same section come in contact, hybrids result. Such a situation undoubtedly occurs in southeastern Oklahoma resulting in hybridizations among P. purpureum, P. pulcherrimum, and P. decumbens. From my greenhouse study, the bybrids seem fully fertile and vigorous but this in no way measures their ability to compete in their natural environments.

Compatability within the four sections tested (Purpurei, Phleoides, Candidi and Villosi) is summarized in Fig. 1. Compatibility within selected members of section Purpurei is summarized in Fig. 2.

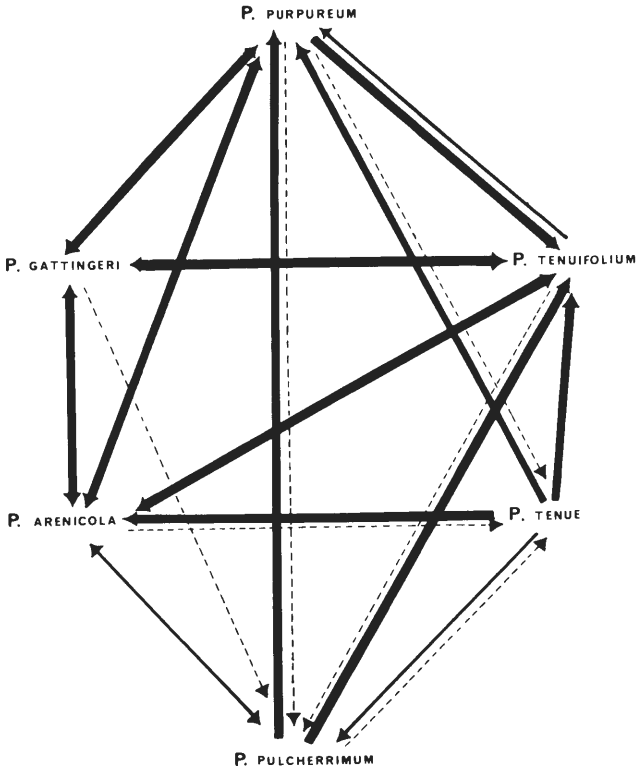


Figure 2. Diagram showing attempted crosses between members of section Purpurei in Petalostemon. The arrows indicate the direction of pollen transfer. Attempted crosses wherein less than 5% seed set resulted are indicated with a broken line. The thin, solid line represents 5-10% seed set. The wide, solid line represents a seed set greater than 10%.

CYTOLOGICAL STUDIES

Cytological studies using root tips and microsporocyte preparations were made on 11 species, 8 interspecific hybrids and 1 F_2 interspecific hybrid. Eight of the species counts have not previously been reported. A summary of my counts and those of other workers is presented in Table 2 and selected illustrations of the meiotic and mitotic figures are shown in Figs. 3, 4. Voucher specimens for each of the counts were deposited in ISC except when otherwise noted.

All counts previously made as well as my own show Petalostemon to possess a diploid number of 14. There were no consistent meiotic abnormalities either in the species or the hybrids that I examined. Occasional examples of binucleate pollen mother cells, such as those reported by Sen and Krishnan in Clitoria ternata (1961), were observed.

An attempt was made to study meiosis in specimens of Petalostemon that were male sterile, but I was unable to observe any meiotic figures in anther preparations from these plants. It is possible that the disturbance resulting in male sterility takes place before meiosis, perhaps in pollen mother cell formation.

POLLEN ANALYSIS

Pollen investigation, particularly those involving size and shape relationships, have heretofore been undertaken mainly by paleobotanists. The topic can hardly be introduced without mention of the works of G. Erdtman (1952, 1954), but the primary focus of these books, even though they have taxonomic implications, is the study of fossil pollen. Two recent papers have pointed out the importance of pollen analysis as an additional tool for the systematist dealing with modern plants (Horton 1963; Stone 1963).

Both Horton and Stone utilized freshly collected pollen for their studies. I used fresh pollen also, but found it is equally feasible, for Petalostemon, to use pollen from herbarium sheets. Drying evidently has little effect on the exine and if the investigator is primarily interested in external dimensions of the grains, 24 hours in lactophenol and cotton blue is sufficient to inflate the grains to their normal size.

The pollen of Petalostemon varies in shape from subprolate to prolate (Erdtman 1954). The larger pollen grains of the section Purpurei tend to be more elongate than those of the other sections that possess smaller, more spheroidal grains. The tricolpate grains appear only slightly sculptured under 430x magnification. They bear no irregularities or protuberances.

To the naked eye the pollen is yellow or orange; the color is due to an orange liquid that adheres to the grains. This substance is immiscible in lactophenol, but has not been further characterized. It is especially prevalent in members of section Purpurei—the species that possess yellow-orange or orange pollen. Representatives of the other sections have yellow pollen.

Pollen fill (or, as it is usually interpreted, viability) as tested with cotton blue, is high in almost all species. In all except P. tenuifolium and P. villosum the number of aborted or nonstaining pollen grains was

Table 2. Chromosome numbers reported in the genus Petalostomen. All counts are 2n. The asterisk (*) indicates previously unreported counts.

Species	References and(or) collection data
*P. albidum	Wemple: Alachua Co., Florida, Isely and Wemple 9257. Columbia Co., Florida, Isely and Wemple 9372.
*P. arenicola	Wemple: Kearney Co., Kansas, Wemple 319.
P. candidum	Ledingham (1957). Turner (1959).
*P. carneum	Wemple: Citrus Co., Florida, Isely and Wemple 9271
*P. pinnatum ssp. pinnatum	Wemple: Alechua Co., Florida, Isely and Wemple 9246.
*P. pinnatum ssp. trifoliatum	Wemple: Holmes Co., Florida, Isely and Wemple 9177. Leon Co., Florida, seeds collected by A. W. Clewell from same location as Clewell 758. No voucher specimen retained.
P. feayi	Turner (1963). Wemple: Highlands Co., Florida, Isely and Wemple 9316.
*P. gattingeri	Wemple: Franklin Co., Alabama, Wemple 470.
P. glandulosum (synonymous with P. phleoides in this treatment)	Turner (1956).
*P. gracile	Wemple: Jackson Co., Mississippi, Isely and Wemple 9110. Mobile Co., Alabama, Isely and Wemple 9115. Baldwin Co., Alabama, Isely and Wemple 9129.
P. griseum	Turner (1959). Turner and Fearing (1960).
*P. microphyllum	Wemple: from seeds collected in Callahan Co., Texas by N. C. Henderson, Wemple greenhouse No. 65B.
P. pulcherrimum	Turner (1956). Wemple: from seeds collected in Travis Co., Texas, Wemple greenhouse Nos. 8J, 8M. Grimes Co., Texas, Wemple and Jackson 717.
P. purpureum	Ledingham (1957). Wemple: from seeds collected in Sumter Co., Alabama, Shinners 12634. From seeds collected in Clark Co., Arkansas, Demaree 38695.
P. stanfieldii (Synonymous with P. tenue in this treatment)	Turner (1956).
*P. tenuifolium	Wemple: from seeds collected in Ochiltree Co., Texas, Wallis 4806.
P. villosum	Ledingham (1957).

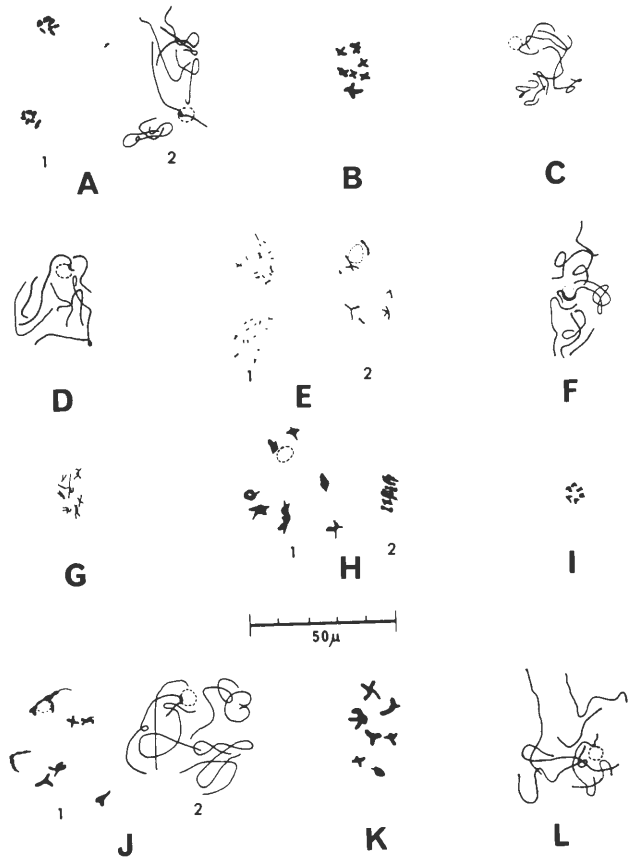


Figure 3. Meiotic and mitotic figures in species of Petalostemon. A. P. albidum; 1. anaphase II, 2. pachytene. B. P. arenicola. C. P. carneum. D. P. pinnatum ssp. pinnatum. E. P. pinnatum ssp. trifoliatum; 1. mitosis (two cells), 2. pachytene. F. P. feayi. G. P. gattingeri. H. P. gracile; 1. diakinensis, 2. metaphase. I. P. microphyllum, anaphase II. J. P. pulcherrimum; 1. diakinensis, 2. pachytene. K. P. purpureum. L. P. tenuifolium.

always less than 1%. P. tenuifolium was unique in that the grains showed wide variations in size and shape. This is indicated by the relatively wide range of both length and width measurements as well as a large standard deviation for both (Table 3, Fig. 5). In addition to size and shape variation, there was invariably 5-15% nonstaining pollen in each sample. P. villosum, while having uniform pollen size, usually showed about 10% nonstaining pollen.

Measurements and their analysis are presented in Table 3 and Fig. 5. The species are grouped according to sections and within the sections,

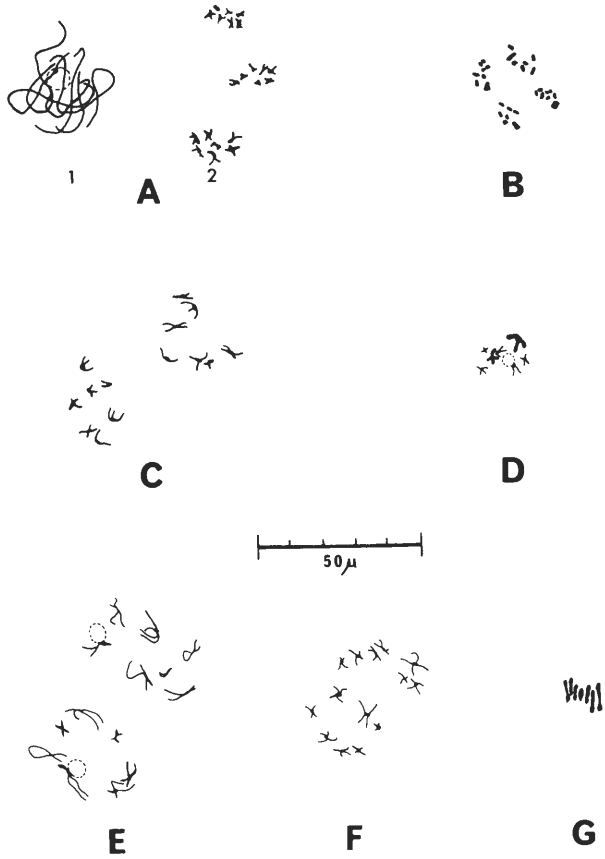


Figure 4. Meiotic figures in interspecific hybrids of Petalostemon. A. P. tenuifolium x P. arenicola; 1. pachytene, 2. anaphase II. B. P. arenicola x P. tenuifolium. C. P. arenicola x P. pulcherrimum, two cells. D. P. arenicola x P. purpureum. E. P. gattingeri x P. tenuifolium, two cells. F. P. pulcherrimum x P. purpureum, two cells. G. (P. tenuifolium x P. arenicola) x self.

on variations in pollen size and shape. It is evident that the measured pollen characteristics coincide with the external morphological characteristics upon which the sections are based.

Several tentative generalizations can be drawn from this data: 1) Members of section Purpurei seem related in the possession of large, prolate pollen grains. 2) The pollen size of P. searlsiae is interesting because this species has many characteristics that suggest that it is allied with the Purpurei—most specifically with P. tenuifolium whose pollen size P. searlsiae closely approximates. The morphological basis for including the latter species in the Ornati rather than the Purpurei

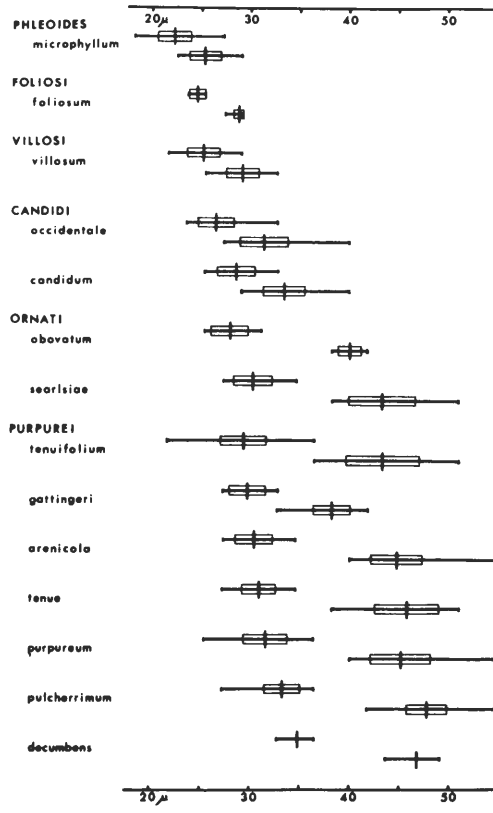


Figure 5. Pollen size and shape analysis of selected species of Petalostemon. Length of the horizontal line indicates the range of variation in width (upper line) and length (lower line). The central cross mark indicates the arithmetic mean for all grains sampled. The rectangle represents + or - one standard deviation.

will be discussed later. 3) Sections Phleoides, Foliosi and Villosi possess small subprolate pollen grains. Morphologically these sections are quite distinct from one another, yet they are unique among the Petalostemon in that they all possess a high leaflet number (15 or more).

I have also examined the pollen of most of the artificial hybrids that I have synthesized as well as that of a naturally occurring hybrid between P. purpureum and P. pulcherrimum [Table 4 (Wemple 402, Marshall Co., Okla.)]. Usually pollen size of the hybrid is intermediate between that of either parent—this intermediacy parallels that shown by the hybrids in other morphological characteristics. Seldom is the viability of the pollen substantially reduced except for all P. tenuifolium hybrids, where the "abnormalities"—size and shape variation and inviability—of the P. tenuifolium parent seem emphasized. This variation was noted in

Table 3. Pollen analysis of species of Petalostemon. Asterisk (*) indicates that all measurements were from dried pollen taken from herbarium specimens

"Section"	Species	No. of samples	No. of plants	Width in μ			Length in μ		
				Range	Arithmetic mean	Standard deviation	Range	Arithmetic mean	Standard deviation
Phleoides	microphyllum	10	7	18-27	22.23	1.61	24-29	26.34	1.62
Foliosi	foliosum	2	2	23-25	24.55	0.93	27-29	28.91	0.55
Villosi	villosum	10	10	22-29	25.23	1.57	25-33	29.09	1.70
Candidi	occidentale	11	8	24-33	26.41	1.79	27-40	31.32	2.47
Candidi	candidum	8	5	25-33	28.61	1.91	29-40	33.39	2.07
Ornati	obovatum	2	2	25-31	28.0	1.81	38-42	39.99	1.18
Ornati	searlsiae*	4	4	27-35	30.27	1.91	38-51	43.18	3.31
Purpurei	tenuifolium	7	5	22-36	29.32	2.26	36-51	43.17	3.68
Purpurei	gattingeri	5	4	27-33	29.78	1.78	33-42	38.15	1.78
Purpurei	arenicola	7	5	27-35	30.49	1.89	40-55	44.75	2.58
Purpurei	[illegible]ue	4	3	27-35	30.95	1.67	38-51	45.77	3.24
Purpurei	purpureum	13	10	25-36	31.01	2.19	40-55	45.01	3.01
Purpurei	pulcherrimum	15	14	27-36	33.24	1.75	42-55	47.84	2.09
Purpurei	decumbens	1	1	33-36	34.91	Not calculated	44-49	46.73	Not calculated

Table 4. Pollen analysis of interspecific hybrids of Petalostemon. SSV indicates that size and shape variation was noted. Abnormalities are indicated in % of the sample that appeared abnormal. Asterisk (*) indicates a field collected hybrid between P. purpureum and P. pulcherrimum (Wemple 402 Marshall Co., Okla.)

Female parent		Male parent	No. of samples	No. of plants	Width in μ. Range	Width in μ. Mean	Length in μ Range	Length in μ Mean	Abnormalities
P. candidum	X	P. occidentale	2	2	25-31	28.0	33-36	33.91	8%
P. tenuifolium	X	P. purpureum	4	3	29-33	31.05	36-47	42.77	SSV, 15-70%
P. purpureum	X	P. tenuifolium	1	1	31-36	32.0	40-51	44.91	5%
P. tenuifolium	X	P. pulcherrimum	1	1	29-33	31.09	44-47	45.64	—
P. tenuifolium	X	P. arenicola	14	13	25-35	29.88	33-47	42.91	SSV
P. arenicola	X	P. tenuifolium	1	1	25-33	30.18	40-46	40.36	SSV
P. gattingeri	X	P. tenuifolium	1	1	29-33	30.36	36-42	39.09	SSV, 20%
P. gattingeri	X	P. purpureum	2	1	25-31	28.82	36-44	36.29	SSV
P. purpureum	X	P. gattingeri	2	2	27-33	30.09	42-51	44.10	SSV
P. arenicola	X	P. gattingeri	1	1	29-31	29.45	38-44	42.54	—
P. arenicola	X	P. purpureum	2	2	29-35	30.91	42-51	46.36	—
P. arenicola	X	P. pulcherrimum	3	3	29-36	32.16	42-51	45.27	—

Table 4 (Continued).

Female parent	Male parent	No. of samples	No. of plants	Width in μ Range	Width in μ Mean	Length in μ Range	Length in μ Mean	Abnormalities
P. pulcherrimum X	*P. arenicola*	3	3	29-36	32.24	40-53	45.51	--
P. purpureum X	*P. pulcherrimum*	1	1	33-35	33.27	42-51	44.73	--
P. pulcherrimum X	*P. purpureum*	2	1	31-36	33.18	36-45	47.84	--
P. purpureum X	*P. tenue*	3	2	29-33	30.61	42-45	42.97	--
402*		3	1	31-36	32.91	47-56	51.15	--
P. tenuifolium X	402*	1	1	29-33	31.09	40-47	44.0	SSV
P. purpureum X	402*	2	2	29-36	32.73	42-47	44.36	30-60%
402* X	*P. arenicola*	1	1	29-33	30.91	47-53	48.91	--
(*P. tenuifolium* X Self	*P. arenicola*) X	3	3	27-33	30.18	40-45	42.54	SSV, 10%
(*P. arenicola* X Self	*P. gattingeri*) X	2	2	27-35	29.91	38-45	39.91	SSV, 5%
(*P. purpureum* X Self	*P. gattingeri*) X	1	1	33-38	34.73	40-45	43.27	40%

crosses with all other species and seemed to hold true regardless of whether P. tenuifolium was used as the staminate or pistillate parent. Data is also presented on a limited number of second generation hybrids, most of which show a high proportion of abnormal pollen grains.

THE GENUS PETALOSTEMON

Petalostemon Michx. Fl. Bor. Am. 2:48. (1803). Nom. Cons.
Type species P. candidum Michx. Type material in P.
Anonymos Walt. Fl. Carol. 102-103 (1788).
Dalea Juss. Gen. Fl. 355. (1789).
Kuhnia Gmel. Syst. Nat. 2:375. (1791) pro parte.
Kuhnistera Lam. Encycl. Meth. 3:370. (1792).
Psoralea Poir., in Lam. Encycl. 5:694. (1804) pro parte.
Gatesia Bertol. Novi. Comm. Acad. Sci. Inst. Bonon. 9:212-214. (1849).
Gavesia Walp. Ann. Bot. Syst. 950. (1852).

Nomenclature

The first specimen of Petalostemon returned to the Old World was collected by Walter (loc. cit.), and described as "Anonymos Kuhnis affinis. pinnat." The following year, Jussieu (loc. cit.) included the Walter species within Dalea—a resurrection of a name used by Linnaeus (1737) in the first edition of Genera Plantarum, but subsequently dropped. Although not mentioning the Walter specimen by name, Jussieu (p. 355) follows the description of Dalea with:

> Speciem habeo siccam, habitu flosculosam Eupatorii instar sed Daleae ferè congenerem cui calix communis polyphyllus imbricatus multiflorus, calix proprius inferus 5-partitus plumosus, petala 5 subaequalia unguiculata, caetera similia.

Ten years later, Ventenat (1799a, p. 395) corroborated the fact that Jussieu was indeed speaking of Walter's plant.

> La plante dont Jussieu donne use courte descriptions apreès avoir exposé les caractères du Dalea, est, selon Michaux, L'Anonymos de Walter.

The first valid publication of a name for Walter's specimen was by Gmelin (loc. cit.). It was placed in the established composite genus Kuhnia as K. pinnata. Lamarck (loc. cit.) applied another binomial, Kuhnistera caroliniensis, to this taxon.

The first lucid statement of the similarities and differences between the Walter specimen and the other species of Dalea was made by Ventenat (1799a). The Lamarck genus Kuhnistera was maintained, but separate from Dalea. Included under the latter genus were both 5 and 10 staminate species, thus amending Jussieu's original generic concept. Although Ventenat cited no species per se, his description of a representative Dalea is clearly that of D. purpurea, a species that he eventually named in 1800.

Ventenat's previously stated views were expanded in Dissertation sur le Genre Dalea (1799b). But again he presented no species names. The

following year (1800), his description of Dalea purpurea appeared. This species, now Petalostemon purpureum (Vent.) Rydb., was described as one of a number of "rare and unusual" plants growing in the gardens of J. M. Cels in Paris. The seeds of this species were evidently collected in Illinois by Michaux several years before and passed into the hands of J. M. Cels.

The year 1803 saw the publication of Michaux' Flora Boreali-Americana. In it Kuhnistera was considered akin to the pentastaminate members of Dalea, and both were included in the new genus Petalostemon. Michaux, or L. C. Richard who wrote the diagnoses for the Flora (Barneby 1965), chose to ignore both prior specific epithets (pinnatum and caroliniensis) for Walter's specimen, although Lamarck's generic name, Kuhnistera, was cited in synonymy. The species was called Petalostemon corymbosum. Other species named were P. candidum, P. carneum and P. violaceum (the last falls within the circumscription of Dalea purpurea, but Ventenat was not cited).

Before the publication of the Flora Boreali-Americana, Willdenow's third volume of Species Plantarum was issued (1802, according to Schubert 1942). Willdenow included species with both 5 and 10 stamens in his delimitation of the genus Dalea, enumerating several with 5 stamens, D. candida (citing P. candidum Michx.) and D. kuhnistera (citing Lamarck as well as Walter).

Poiret (loc. cit.) included all the aforementioned species with the 10-staminate daleas in the genus Psoralea, a treatment similar to the later works of Linnaeus. Subsequently, he again rejected the idea of a separate generic ranking for the pentastaminate species (Poiret 1818, p. 459).

> Le genre Petalostemum de Michaux ne peut etre séparé des dalea, quoique ses fleurs ne renferment souvent que cinq étamines, seul caractère qui le distingue.

He recognized D. purpurea, D. carnea, D. candida, and D. corymbosa.

In summary: As of 1818, the species of the taxon, herein called Petalostemon, had been placed under five different generic names, Kuhnia, Kuhnistera, Petalostemon, Dalea, and Psoralea. No subsequent authors have included the species as a part of Psoralea; that genus was later more precisely defined to exclude those species possessing only one flower per subtending bract, pinnate leaves composed of more than three leaflets and petals inserted anywhere other than at the floral base. Except for Shinners (1949a, b), no authors have included the species of Petalostemon within Dalea—although Barneby (1965) strongly argues for their merger. Rather, Dalea has been limited to species possessing (7) 9-10 stamens, a more or less papilionoid corolla and petals inserted either at the floral base or part way up on the androecial tube—a definition more in line with that of Michaux than that of Jussieu. Barneby (1965), in fact, recommended conservation of Dalea, sensu L. C. Richard in Michx. over other definitions of the genus.

Petalostemon was adopted for all the pentastaminate species by most 19th and 20th century authors; e. g., Pursh (1814), Candolle (1825), Don (1832), Torrey and Gray (1838) and Endlicher (1840) among classical treatments. Others maintained both Petalostemon and Kuhnistera as

separate genera [e.g., Bartling (1830) and Lindley (1853)]—a practice continued into the present century by Small (1903, 1933), Rydberg (1919-1920) and, most recently, Hutchinson (1964).

Kuntze (1891) revived Kuhnistera in place of Petalostemon on the basis of its prior publication and made new combinations for the 19 species known at that time. As one of the adherents to the American code who adopted Kuhnistera, Heller published "Notes on Kuhnistera" (1896), a definitive work at that time. This treatment included 22 species with critical synonymy and nomenclatural notes. The next complete treatment of the genus was by Rydberg (1919-1920), who, as indicated, separated Petalostemon from Kuhnistera; he included 42 species in the former and 2 in the latter. This was the last complete summary of the genus to this date, although Isely (1958) in a generic summary of the tribe Psoraleae reconsidered the problems in the delimitation of the genus. Since the conservation of Petalostemon over Kuhnistera (Briquet 1912), all authors employed Petalostemon, at least for the species other than P. pinnatum and P. adenopodum. Kuhnistera has been maintained as a separate genus by Rydberg (1919-1920), Small (1903, 1933) and Hutchinson (1964) as previously stated. Isely (1958) as well as authors of two recent Carolina floras, Wilbur (1963) and Radford, Ahles and Bell (1964), unite all species under Petalostemon.

Gatesia Bertol. and its orthographic error, Gavesia Walp., was applied to what I consider P. pinnatum trifoliatum. An extended discussion of this name may be found in the nomenclatural section for the subspecies.

There has been controversy over alternative spellings of the noun Petalostemon as well as interpretation of the gender (masculine or neuter). Michaux originally used the spelling Petalostemum in conjunction with neuter specific epithets. Most authors since the original publication have used Petalostemon, some considering it masculine, others neuter. Rydberg (1919-1920) comments in a footnote, "Originally published as Petalostemum, but incorrect as στημων is masculine and has a long o in the final syllable." Shinners (1949a, p. 81) employed Michaux' original spelling and adds a footnote:

> In the list of nomina conservanda making up the Appendix III of the International Rules of Botanical Nomenclature (cf. Brittonia 6:67, 1947), this is altered to the etymologically proper form of Petalostemon—in flagrant violation of Article 59 of the same Rules, expressly forbidding such corrections!

I have herein adopted both the spelling and gender indicated by the Nomina Generica Conservanda in the citation of the generic type, Petalostemon candidum.

Generic description

Perennial, glandular-punctate herbs with many stems arising from a well-developed taproot or caudex. Stipules subulate. Leaves usually with smaller leaves or reduced stem systems in their axils, odd-pinnate, with (3) 5-numerous leaflets; leaflets usually narrow to elliptical but sometimes broad and almost ovate, usually ± involute. Flowers in terminal, globose to cylindrical spikes, each flower subtended by a conspicuous bract that usually exceeds the length of the calyx in bud; the flowers of some species also with bracteoles flanking the base of the

calyces. Calyx campanulate to tubular, 3.0-7.7 mm long (including lobes), sometimes oblique; the lobes deltoid to lanceolate or, less frequently, filiform-plumose. Standard long-clawed, arising from a socket near the floral base, the blade oblong to cordate; the four other petals arising from the apex of the staminal tube, or very slightly below, interdigiting with the 5 monadelphous stamens; claws inserted in prominent sockets; blades strap-shaped to oblong, spreading from the floral axis. Free portions of the filaments usually diverging from the floral axis, equaling or exceeding the length of the androecial tube and usually subequal to the petal apices at anthesis. Ovary globose to elliptical, 2-ovulate; the style equaling or exceeding the petal apices and anthers shortly after anthesis. Pod ovate to lunate, 1-seeded; the stylar beak offset to the standard side of the calyx at maturity. The indehiscent legume falling enclosed in the calyx.

Distribution

Ranging from northern Mexico throughout much of the United States north to southern Canada. The greatest number of species is found in Texas. One complex extends from the Great Basin northward into the Pacific Northwest. Another is found in the southeastern states. The principal area in which Petalostemon is absent is the northeastern deciduous forest.

Key to the subgenera

1. Spikes subglobose, compact, disposed in a corymbose manner, surrounded by a series of oval to reniform, sterile bracts; calyx lobes filiform and plumose; flowers white; restricted to the southeastern states. I. Kuhnistera

1. Spikes various, rarely subglobose or corymbosely disposed, seldom with sterile bracts at the base of the spikes; calyx lobes deltoid or lanceolate; flowers variously colored, not restricted to the southeastern states. II. Petalostemon

I. Subgenus KUHNISTERA (Lam.) Wemple comb. nov.
Kuhnistera Lam. Encycl. Meth. 3:370. (1792).

Introduction

The three taxa composing subgenus Kuhnistera are united by the possession of three distinctive characteristics: 1) subglobose, compact spikes surrounded by a series of oval to reniform, sterile bracts; 2) spikes disposed in a corymbose manner; and 3) filiform and plumose calyx lobes. None of these characteristics is unique within Petalostemon, but their combination in this geographically restricted trio of species clearly sets this subgenus apart. The plants are endemic to the southeastern Coastal Plain of southern Mississippi, Alabama, Florida, Georgia, South Carolina and North Carolina. Within this area they are found only on the more elevated, drier, sandy areas, locally called "sandhills." They are usually associated with pines and scrub oaks. Ecologically they are sympatric through part of their range with Petalostemon albidum and P. feayi. They are the only species of Petalostemon with representation in the Carolinas.

Meiotic and mitotic preparations of P. pinnatum yield 7 and 14 chromosomes, respectively, consistent with the rest of the genus (Table 2, Fig. 3D, E). Pollen collected from P. pinnatum ssp. trifoliatum, (Isely and Wemple 9177), Holmes County, Florida, appeared typical of the genus, in length averaging 29 microns, in width 20 microns.

Key to the Species

1. Leaflets over 2 mm wide; stems with spherical, protuberant "glands" becoming more numerous toward the apex of the stem; limited to the Florida peninsula. 1. P. adenopodum

1. Leaflets less than 2 mm wide, generally filiform; "glands" present on the stem but not spherical-protuberant; not limited to the Florida peninsula. 2. P. pinnatum

1. PETALOSTEMON ADENOPODUM (B. L. Robs. ex Rydb.) Wemple (Map 1, Fig. 6 A-H).

Petalostemon adenopodum (B. L. Robs. ex Rydb.) Wemple. Based on Kuhnistera adenopoda B. L. Robs. ex Rydb. [Improperly published as Kuhnistera adenopoda (B. L. Robinson) Rydberg. N. Am. Fl. 24: 136. (1919-1920)].

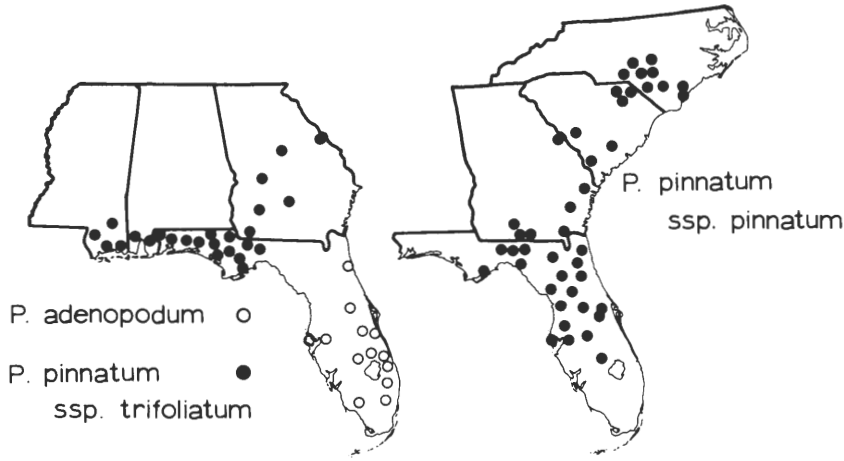
Petalostemon corymbosum adenopodum B. L. Robs. M.S. in herb. Type in GH. (1).

Kuhnistera truncata Small. Bull. Torr. Bot. Club 51:380-381. (1924). Type material in NY. (2)

Nomenclature

This species was first described by Rydberg (loc. cit.) who based his name on a B. L. Robinson annotation label. The type sheet is a mixture of P. adenopodum and P. pinnatum ssp. pinnatum. Robinson identified both on the annotation label as respectively: "P. corymbosum, var. adenopodum, Rob. n. var." and "P. corymbosum, Michx. typical form." Rydberg's description is headed by: "2. Kuhnistera adenopoda (B. L. Robinson) Rydberg sp. nov.," giving Robinson full credit for the specific epithet even though it was not validly published. I have designated the citation as, "Robs. ex Rydb.," a procedure possibly not without question, but it seems the most logical course. Rydberg limits the species to the Tampa Bay Region of Florida's west coast, the location of the original Garber collection on which the name was based.

Small proposed the species Kuhnistera truncata based on an F. C. Rane collection at Earman, Florida, March 2, 1921, also citing other collections along the east coast of Florida at Jupiter, "many years ago," by C. Hitchcock. Small's discussion is confusing since he begins with an acknowledgment of Rydberg's K. adenopoda and then compares his species with K. pinnata (P. pinnatum) rather than K. adenopoda. He comments on the difference in leaflet width and the more open inflorescence in his species, but attaches special emphasis to the truncate petals. He makes no explicit comparison with K. adenopoda. Had he done so, he would have found no essential differences. With regard to petal shape, I have examined petals of specimens throughout the range of P. adenopodum including several sheets annotated in Small'e hand, "K. truncata."



Map 1. Geographic distribution of the species of subg. Kuhnistera.

Fig. 6 shows examples of the variation found. There seems no correlation between petal conformation and distribution. In contrast to P. pinnatum, the petal shape is quite different, as Small points out. It is possible that Small, in studying specimens from the east coast of Florida and presuming that Rydberg's species, K. adenopoda, was restricted to the west coast, cast around for a character on which to base a new species and seized on the seeming variation in petal shape.

Description

Plants lacking a prominent caudex, the root often red. Stems dark, glabrous and striate, 1 m or shorter, covered with spherical, protuberant secretory cavities ("glands") about 1 mm in diameter, increasing in abundance toward the stem apex. Leaves fascicled, less than 2 cm long with 3—7 elliptical leaflets, usually 2—3 mm wide and 6—8 mm long, paler green on top surface, often involute. Inflorescence corymbose with peduncles below the individual flower spikes lacking, the leaves gradually merging into involucral-like, oval to reniform, sharply acuminate, ciliate, sterile bracts. Calyx villous, tube 2—3 mm long, lobes plumose, 4.0—4.5 mm long. Corolla white, standard lanceolate, sometimes truncate, 0.8 mm wide, 3.5 mm long, equaling claw; apical petals lanceolate, sometimes truncate, blades 1.0 mm wide, 3.0 mm long, claw 1.2 mm long. Androecial tube 5—6 mm long, almost equaling tips of calyx lobes, stamen filaments 4.0 mm long, spreading at anthesis. Ovary 2.0 mm long, bearded on the distal 2/3, predominantly so on the upper surface; style 10.0 mm long bearded proximally over 1/2 its length.

Distribution and phenology

Restricted to the lower half of peninsular Florida.[1] Limited to the

[1] A northern extension to the range is suggested by three collections from St. Johns county in Northeastern Florida. All are collections of Mary C. Reynolds (1874-1877). The labels state St. Augustine, Florida. It is possible that this was her place of residence and not necessarily the location where the plants grew.

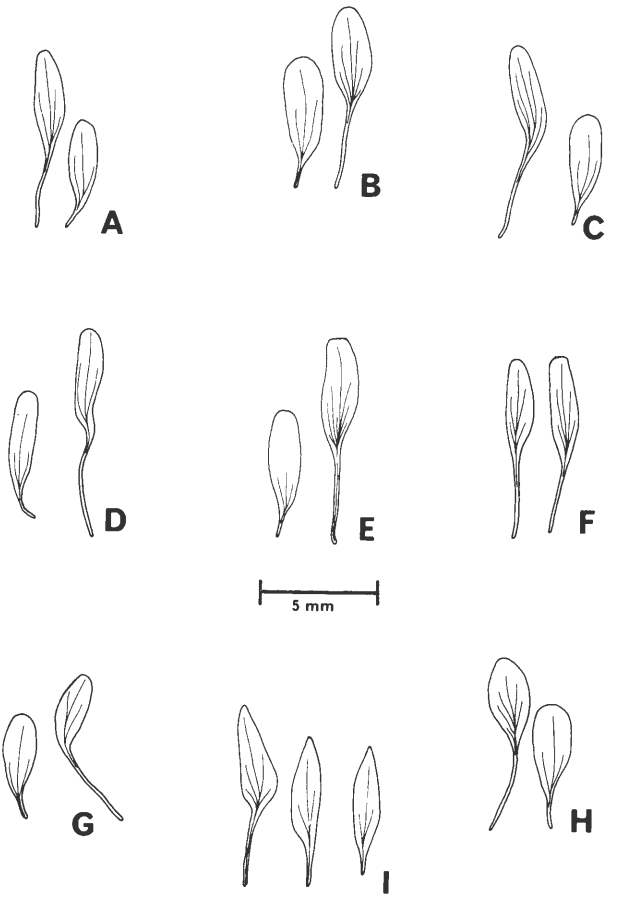


Figure 6. Petal variation in subgenus Kuhnistera.
A—H, apical petals and standards of P. adenopodum.
I, apical petals and standard of P. pinnatum ssp. pinnatum.

A. Garber year 1887, Hillborough Co., Fla. (isotype of P. adenopodum).
B. Schallert 20850, Orange Co., Fla.
C. Reynolds 10025, St. Johns Co., Fla.
D. Deam 2817, Pinnelas Co., Fla.
E. Small 2307, St. Lucie Co., Fla.
F. West and West 4 Nov. 1945, Martin Co., Fla.
G. Harden et al. 14080, Collier Co., Fla.
H. Kent 24 Oct. 1942, Broward Co., Fla.
I. P. pinnatum ssp. pinnatum, Young, South Carolina.

higher, drier sandy areas. Often associated with turkey oak (Quercus laevis Walt.), long leaf pine (Pinus australis Michx.) and saw palmetto (Serenoa repens Small), a habitat similar to that occupied by P. pinnatum to the north. Geographically and ecologically sympatric in part of its range with P. feavi.

Anthesis is from mid-September to late November.

The poor representation of this species in major herbaria perhaps represents as much a paucity of collectors as a rarity of the plants (see Shinners 1964). During 2 days collection across peninsular Florida, P. adenopodum appeared common in its preferred habitat.

2. PETALOSTEMON PINNATUM (Gmel.) Blake

Description

Stems slightly branching, up to 1.1 m tall; moderately striate, glabrous with "glands" prominent but not protruding above the surface of the stem and not increasing in number toward the stem apex. Leaves fascicled, 1—2 cm long, bearing 3—13 linear-filiform, usually involute leaflets less than 0.9 mm broad. Inflorescence corymbose, simple or compound; peduncles below the individual flower spikes lacking, the apical leaves merging into several whorls of oval to suborbicular, ciliate-acuminate, sterile bracts. Flowers disposed in compressed spikes. Calyx villous, tube 2 mm long, lobes plumose-filiform, 3—6 mm long. Corolla white, standard lanceolate, cuneate at the base of the blade, 1 mm wide, 4 mm long, equaling the claw; apical petals similar to the standard but with claws only 1.0—1.5 mm long. Androecial tube 5 mm long, the free portions of the filaments 5—6 mm long. Ovary 2 mm long, the style 10 mm, both bearded.

Key to the subspecies

1. Leaflets 5—13; spikes arranged in a compound corymb; ranging through northern peninsular Florida, western Georgia, South Carolina and North Carolina. 2a. P. pinnatum ssp. pinnatum

1. Leaflets 3; spikes arranged in a simple corymb; limited to southern Alabama, southern Mississippi, the panhandle of Florida and central Georgia. 2b. P. pinnatum ssp. trifoliatum

2a. PETALOSTEMON PINNATUM SSP. PINNATUM (Gmel.) Blake
(Map 1, Fig. 61)

Petalostemon pinnatum (Gmel.) Blake. Rhodora 17:131. (1915). Based on Anonymos pinnat. Walt.

Anonymos Kuhnia affinis pinnat. Walt. Flor. Carol. 102-103. (1788). Type at BM. (1) (2).

Kuhnia pinnata Gmel. Syst. Nat. 2:375. (1891). Based on Anonymos pinnat. Walt.

Kuhnistera caroliniensis Lam. Encycl. Meth. 3:370-371. (1792). Based on the description of Anonymos pinnat. Walt.

Dalea kuhnistera Willd. Sp. Pl. 3:1337. (1802). Based on Kuhnistera caroliniensis Lam.

Petalostemum corymbosum Michx. Flor. Bor. Am. 2:40. (1803). Based on Anonymos pinnat. Walt.

Psoralea corymbosa Poir. in Lam. Encycl. 5:694-695. (1804). Based on Petalostemon corymbosum Michx.

Kuhnistera pinnata (Walt.) Kuntze. Rev. Gen. 1:192. (1891). Based on Anonymos pinnat. Walt.

Petalostemum caroliniense (Lam.) Sprague. Kew Bull. 1939:331.

Nomenclature

As previously discussed in the historical review of the genus, there have been many names applied to this taxon. The first specific epithet proposed by Walter (pinnatum) was published in the "genus Anonymos." The Anonymos names are outlawed by Article 20 of the Code of Botanical Nomenclature (Lanjouw 1961), and the Blake combination in Petalostemon was not made until 1915. Gmelin, however, in 1791 used this specific epithet under the genus Kuhnia following the established line of thought at the time that the specimen was a Composite.

Sprague (loc. cit.) based his combination P. caroliniense on the Lamarck publication presumed to be published in 1789. The recent work by F.A. Stafleu (1963) dates Lamarck's volume as 1792 rather than 1789 when the series started. Hence, the (Gmel.) Blake combination should be adopted. I am indebted to Mr. Rupert Barneby for calling the correct publication date of this volume to my attention.

Observations

Subspecies pinnatum is distinguished from subspecies trifoliatum by possessing more than three leaflets and having the spikes disposed in a compound rather than a simple "corymb." The range of the two is for the most part distinct, but they are sympatric in Franklin and Leon counties in the panhandle of Florida and in Richmond county in northeastern Georgia. Subspecies pinnatum throughout its southern range usually has 5 to 9 leaflets, but specimens with a higher leaflet number, 11-15, occur in the more northern part of the range, particularly South Carolina. Usually the leaflets are involute, presenting an almost filiform appearance. Three collections from South Carolina lack involute leaflets, and the plants look remarkably different until one realizes that the leaflets are simply flat rather than tightly rolled. It is possible that these represent a geographic variant of this taxon. The northern populations also frequently show a less well-developed inflorescence, some even possessing a simple "corymb" as found in subspecies trifoliatum.

Distribution and phenology

A common plant of the high, dry, white sand scrub. Ranging from central peninsular Florida, where it replaces the more southern P. adenopodum, through eastern Georgia and the Carolinas. Consistently associated with long leaf pine (P. australis) and turkey oak (Q. leavis) and, throughout its Florida range, the Petalostemon albidum.

Anthesis, September to early November.

2b. PETALOSTEMON PINNATUM SSP. TRIFOLIATUM (Chapm.) Wemple (Map 1, Fig.10C)

Petalostemon pinnatum ssp. trifoliatum (Chapm.) Wemple. Based on Petalostemon corymbosus var. trifoliatus Chapm.

Petalostemon corymbosus var. trifoliatum Chapm. Fl. S.U.S. 100-101. (1897). Type in US. (1)(2).

Gatesia alabamensis Bertol. Novi Comm. Acad. Sci. Inst. Bonon. 9:212-214, Tab. x fig. 1. (1849). Type destroyed at BOLO during World War II. (2).

Gavesia alabamensis (Bertol.) Walp. Ann. Bot. Syst. 950. (1852). Based on Gatesia alabamensis Bertol. (2).

Nomenclature

Chapman, in presenting variety trifoliatus, separates it from the typical P. corymbosus on the following characteristics: 1) it is glandless or nearly so; 2) it possesses 3-4 broadly ovate, acute bracts; 3) the style is ciliate below the middle; 4) the petals are acute; and 5) the leaves are "mostly" trifoliate. To my observation, the two subspecies are indistinguishable in all the aforementioned characteristics except the last. Although Chapman did not cite a type or even a type locality, his numerous collections of this taxon (4-NY, 3-US, 3-MO) clearly indicate his understanding of it. I accept a lectotype, his No. 6097, October 1897, Apalachicola, Florida (US 335288). A duplicate of this collection is at NY.

Gatesia alabamensis Bertol. was described from a plant collected in Alabama and named in honor of the collector, Dr. Gates. The region of collection would indicate that it belonged in subspecies trifoliatum, although the description does not indicate the leaflet number. A colored drawing following the article plainly shows trifoliate leaves but a compound corymb. Throughout the range of subspecies trifoliatum, there are occasional individuals possessing compound corymbs. Their occurrence seems to have no geographic basis, and they always possess trifoliate leaves. Assuming the accuracy of the artist, this is perhaps one of them. Since the type specimen was destroyed at Bologna during World War II (R. Savelli, pers. comm. 1964), this question may never be answered.

Gavesia appears to be merely an orthographic error, a substitution of "v" for a "t." Walpers (loc. cit.) gives Bertoloni full credit for the original name but places it in synonymy.

Distribution and phenology

Limited to southern Mississippi, southern Alabama, the panhandle of Florida and extending northward through the interior of Georgia. Apparently occupying a similar habitat to that of subspecies pinnatum but to the west of that species. Associated with long leaf pine (P. australis) and turkey oak (Q. leavis) and ecologically sympatric with P. gracile, but occupying a different habitat. Anthesis from early September to late October.

As one travels from west to east through southern Mississippi, Alabama and the panhandle of Florida, a gradient in anthesis time is obvious; the more easterly plants bloom several weeks earlier than the western populations.

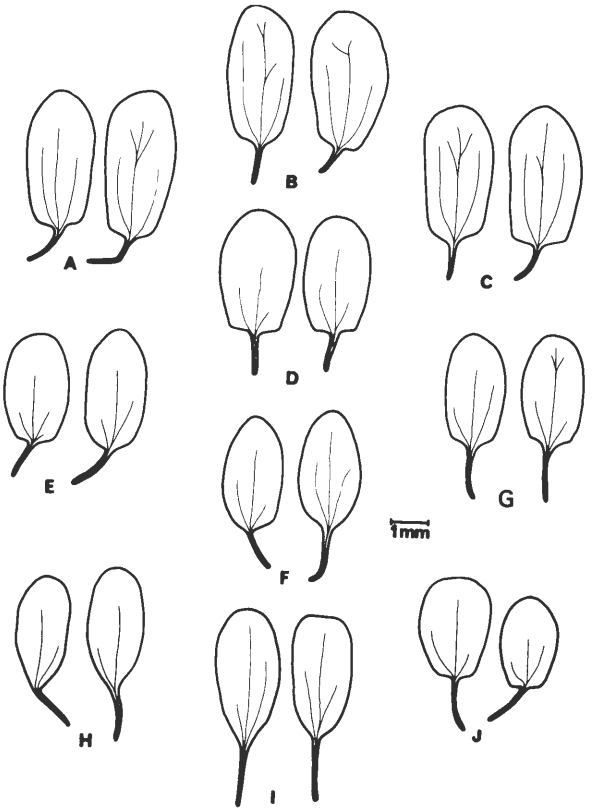


Figure 7. Variations in apical petals of Petalostemon occidentale throughout its range. A—C. Petals of specimens annotated in Rydberg's hand as P. truncatus. D—I. Petals of P. occidentale.
A. Pringle 1216, Guerrero, Chihuahua (US). B. Pringle 1216, Guerrero, Chihuahua (NY). C. Nelson 7248, below Pacheco, Chihuahua. D. Warnock 323, Brewster Co., Texas. E. Livingston 496, El Paso Co., Colorado. F. Rydberg 1480, Hooker Co., Nebraska. G. Stevens 998, Greer Co., Oklahoma. H. Rydberg 59, Deuel Co., Nebraska. I. Wemple 3.5 rootstock in cultivation from Woodbury Co., Iowa. J. Wemple 165A, seedling in cultivation, the progeny of Wemple 3.5.

Figure 8. Type specimen of Petalostemon arenicola Wemple. Deposited in ISC.

II. Subgenus PETALOSTEMON Michx. Fl. Bor. Am. 2:49. *1803).

Key to the Sections

1. Calyx glabrous throughout or villous-ciliate on the lobes only (in P. occidentale and P. microphyllum puberulent overall); bracteoles usually present flanking the base of the calyces.
   2. Mature stem leaves with 3-11 leaflets.
      3. Calyx slit dorsally to 1/2 its length; standard blade not lobed at base, the claw over twice as thick as the apical petal claws; limited in distribution to the southeastern United States. A. Carnei
      3. Calyx not slit dorsally to 1/2 of its length. standard blade basally lobed, the clas the same diameter as the apical petal claws; not limited to the southeast.
         4. Corolla rose-purple; known only from New Mexico. B. Scariosi
         4. Corolla white; not restricted as above. C. Candidi
   2. Mature stem leaves with more than eleven leaflets.
      5. Corolla rose-lavender, apical petals not strap shaped. D. Foliosi
      5. Corolla white, apical petals strap shaped. E. Phleoides
1. Calyx densely pubescent, at least on the angles and lobes; bracteoles lacking.
   6. Stems and leaves spreading pubescent to villous; leaflets 11—21; all species restricted to sandy soils. F. Villosi
   6. Stems and leaves glabrous to glabrate (spreading pilose in P. obovatum); leaflets 5—11(13); not all species restricted to sandy soils.
      7. Leaves solitary, seldom fascicled; leaflets broad elliptical to almost ovate, seldom involute; spikes often subtended by sterile bracts; fertile bracts with scarious margins; calyces spreading sericeous-pubescent. G. Compacti
      7. Leaves fascicled; leaflets linear, involute; spikes not subtended by sterile bracts; fertile bracts seldom with scarious margins; calyces with short appressed or rarely spreading pubescence. H. Purpurei

A. CARNEI

Distinguishing characteristics

Plants glabrous except for pubescence on margins and inner surface of the calyx lobes. Leaflets 3—9 (11). Peduncles usually interrupted by sterile bracts below the spikes. Calyces flanked by a pair of bracteoles arising from the subtending bract; calyx tube slit dorsally more than half

its length. Corolla white or pink, the standard claw over twice as thick as the apical petal claws. Flowering in mid or late summer.

Distribution

Restricted to extreme southeastern Louisiana, southern Mississippi and Alabama, Florida and Georgia.

Observations

Four species are recognized in this southeastern complex. P. feayi is distinct from the other three on the basis of several unique characters. The remaining three are differentiated easily by utilizing multiple characteristics. The intermediacy of P. albidum between P. gracile and P. carneum in many characteristics suggests that P. albidum is possibly of hybrid origin. Support for this hypothesis is also found in the habitat occupied by P. albidum—disturbed areas—which possibly came into existence with the advent of man; the geographical distribution of P. albidum, intermediate between the putative parents; and, the discovery of introgressive populations. That P. feayi has not entered into active hybridization with the other three species is indicated by its uniformity in many characteristics.

A detailed analysis of this complex of species has been undertaken and will be published at a later date.

Cytology

The gametic chromosome number is uniformly n = 7 in the four species (Table 2, Fig. 3, A, C, F, H). Although a determination on P. feayi has been previously reported (Turner 1963), those for the other three species are new. All counts were made from field collections and drawings were made of meiotic figures in pollen mother cells at pachytene, diakinesis, metaphase or incipient tetrad stages. Without exceptions, pairing was normal as was cytokinesis. Voucher specimens were deposited at ISC.

Key to the Species

1. Flowers white; ranging from southern Mississippi through the panhandle of Florida, central and southern Georgia and the Florida peninsula.

   2. Stems weak, usually less than 1.1 mm thick at the base; leaves remote, not fascicled, leaflets 7—9, usually 2 mm or more wide, rachis extension beyond the apical pair, 0.8 mm or greater; peduncles short, usually less than 50 mm, with bracts less than 2 mm long, buds with bract tips recurved; limited to the Florida panhandle and southeastern Georgia, southern Mississippi and southern Alabama. . P. gracile

   2. Stems stout, usually greater than 1.1 mm at the base; leaves close and fascicled, leaflets 5—7, usually less than 2 mm broad, rachis extension less than 0.8 mm; peduncles usually 50 mm or longer with bracts longer than 2 mm; buds with straight bracts; central and southern Georgia and the Florida peninsula. 4. P. albidum

1. Flowers pink; peninsular Florida and Southern Georgia.

3. Spikes cylindrical; bracts longer than the calyx tube; anthers equaling petals at anthesis. 5. P. carneum

3. Spikes globose; bracts shorter than the calyx tube; anthers exserted beyond the petal apex. 6. P. feayi

3. PETALOSTEMON GRACILE Nutt. (Map 2)

Petalostemon gracile Nutt. Jour. Acad. Nat. Hist. Phil. 7:92. (1834). Type in PH. (1) (2).
Petalostemum bicolor Bertol. Mem. Acad. Sci. Inst. Bologna 2:273-274 + illus. pl. 13, f. 1. (1850). (2).
Kuhnistera gracilis (Nutt.) Kuntze. Rev. Gen. Pl. 1:192. (1891). Based on Petalostemon gracile Nutt.

Description

Root with strong napiform development from which radiate multiple, usually unbranched, weakly assurgent, usually nonstriate stems, 3—6 dm long and 0.6—1.3 mm in diameter. Internodes at the middle of the stems 9—32 mm in length, usually longer than the leaves. Leaves solitary at the nodes, usually subtended by a single rib, gradually fading basally into the round stem; rachis from 8—22 mm long, extending beyond the terminal pair of leaflets 0.7—2.8 mm. Leaflets on mature leaves 7—9, glabrous, 5.5—12.0 mm long, 1.2—3.8 mm broad, always less than 5 times as long as broad, elliptical to elliptical-oblanceolate. Peduncles 0.4—10.8 cm long, with sterile bracts up to 2.8 mm in length disposed at varying distances below the spikes. Spikes columnar, 6—15 mm long, 6—8 mm wide, about 1.5 times as long as broad. Bracts elliptical, equaling or slightly less than the lobes at anthesis, the tips usually recurved, a pair of subulate, often ciliate bractioles arising from the base of each. Calyx tubular, slit dorsally to more than half its length; the tube 1.9-2.6 mm long, glabrous, glistening white, the rachis attachment point below the longitudinal calys axis; ventral lobe 0.5—1.2 mm long, green, fleshy and pubescent on the inner surface and margins; glands apparent at the base of the lobes on drying. Corolla white, the standard shorter than the other petals and relatively narrow, the blade 1.1—1.9 mm wide, rounded at the apex; the claw 3—4 times as thick as the claws of the apical petals. Apical petals uniform in shape, the two medial petals inserted lower than the two lateral petals; claws 1.2—2.9 mm in length; blades 1.3—2.9 mm long. Staminal tube not exserted beyond the calyx lobes, filaments shorter than petals, anthers yellow. Ovary always glabrous, style bearded proximally to 1/3—1/2 its length, predominantly on the lower surface.

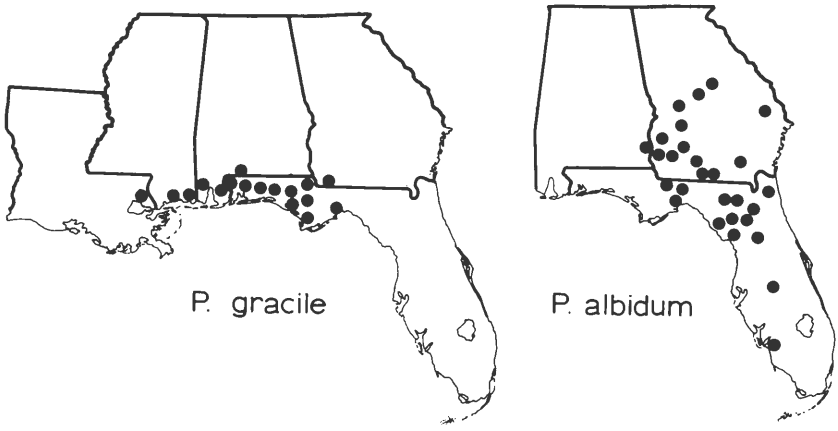
Distribution and Phenology

Petalostemon gracile is limited to southern Mississippi, southern Alabama and the panhandle of Florida. Anthesis is from mid-August through September.

Observations

Petalostemon gracile is commonly found in low grassy areas in association with uncut, long leaf pine (P. australis). On several occasions it was found growing in close proximity to Sarracenia bogs. It was never collected in disturbed habitats.

P. gracile has a very short flowering period as compared with the closely related species, P. carneum and P. albidum. This is dictated in part by the fact that the major stems of P. gracile rarely branch; hence, there is seldom more than one terminal flower spike for each shoot. Additionally, anthesis of all the spikes on a plant begins almost simultaneously.



Map 2. Geographic distribution of Petalostemon gracile and P. albidum.

4. PETALOSTEMON ALBIDUM (T. and G.) Small (Map 2)

Petalostemon albidus (T. and G.) Small Fl. SE. U.S. 630. (1903). Based on Petalostemon carneum β albidum T. and G.
Petalostemon carneum β albidum R. and G. Fl. N. Am. 311. (1838). Type in NY. (1) (2).
Petalostemon carneum of Ell. Bot. S. Carol. and Georgia. 2:176. (1821-1824). (2). non P. carneum Michx. 1803.

Description

Stems numerous, prostrate to erect, 6—10 cm long, 1.0—2.6 mm in diameter, usually subtended by three ribs; leaf rachis 7—22 mm in length, extension beyond the terminal pair of leaflets less than 0.8 mm; leaflets 3—7, commonly 5, involute, 5—12 mm in length, 0.9—2.0 mm wide, usually about six times as long as wide. Peduncles 5—120 mm long with pronounced glands at the apex; peduncular bracts to 5.5 mm long. Spikes columnar, 8—22 mm long, 6—9 mm wide. Bracts equaling or exceeding the calyx lobes at anthesis, lanceolate, usually with straight tips, the base flanked by subulate bracteoles. Calyx tubular, glabrous except for inner surfaces of the lobes, entire calyx 2.7—4.0 mm long, the tube 2.1—3.0 mm long and the ventral lobe 0.5—1.1 mm long. Corolla white; standard with claw 2—3 times as thick as apical petal claws, blade wider than apical petal blades, 1.2—2.9 mm wide; apical petals with blades 1.8—3.3 mm long, claws 1.0—1.9 mm long; claws about half the length of the blade. Androecial tube seldom exserted beyound lobes, anthers yellow, usually equaling the petal apices following

anthesis. Ovary always ± bearded, the style bearded proximally from one-third to more than half its length.

Distribution and Phenology

Petalostemon albidum ranges down through Lee county in southern Florida and north-northwest into central Georgia. Anthesis occurs from early August through September.

Observations

P. albidum is restricted to relatively dry, higher, often disturbed habitats—cut-over areas—and particularly in association with turkey oak (Quercus laevis). It was in one such disturbed area that a "hybrid swarm" was found indicating introgression with P. carneum. Intermediacy of the range of P. albidum between that of P. gracile and P. carneum as well as this preference for a "hybridized habitat" in comparison with the older habitats of the last two species suggests the hypothesis of hybrid origin of P. albidum.

The flowering period is somewhat longer than that of P. gracile partially because of moderate development of axillary branches. After the main apex has flowered, the lateral branches subsequently bloom.

5. PETALOSTEMON CARNEUM Michx. (Map 3; Fig. 9, D, 4)

Petalostemum carneum Michx. Fl. Bor. Am. 2:49. (1803). Type in P. (1) (2).

Psoralea carnea (Michx.) Poir. in Lam. Encycl. 5:694. (1804). Based on Petalostemum carneum Michx.

Dalea carnea (Michx.) Poir. Dict. Sci. Nat. 12:462. (1818). Based on Petalostemum carneum Michx.

Petalostemon roseum Nutt. Am. Jour. Sci. 5:298. (1822). Type in GH. (1) (2).

Kuhnistera carnea (Michx.) Kuntze. Rev. Gen. Pl. 1:192. (1891). Based on Petalostemum carneum Michx.

Kuhnistera rosea (Nutt.) Kuntze. Rev. Gen. Pl. 1:192. (1891). Based on Petalostemon roseum Nutt.

Description

Stems many, erect, 5—10 dm long, fine-striate, usually branched above, 1.5—5.5 mm thick; internodes 3—23 mm long. Leaves fascicled, The rachis 6.5—23.0 mm long, often curving when dried, extending less than 0.8 mm beyond the terminal pair of leaflets; leaves subtended by three stem ribs, or ribs lacking—never a single rib; leaflets 5—11, usually 9, moderately involute, 5—11 mm long and 1—3 mm wide, usually about five times as long as wide. Peduncles from 11-200 mm long, usually glandular at the apex; peduncular bracts subulate, 0.8—6.0 mm long. Spikes columnar, 10—31 mm long and 7—10 mm wide. Bracts usually equaling lobes at anthesis, lanceolate with straight tips, their base flanked by subulate bracteoles. Calyx tubular becoming strongly ribbed upon drying, glabrous except for inner surfaces of the lobes and their margins, entire calyx 3.3—4.7 mm long, the tube 2.2—3.4 mm long and the ventral lobe 0.8—1.8 mm long. Corolla pink. the standard blade orbicular, emarginate and wider than the apical petal blades, 1.2—2.9 mm wide, the claw twice as thick as the claws of the apical petals;

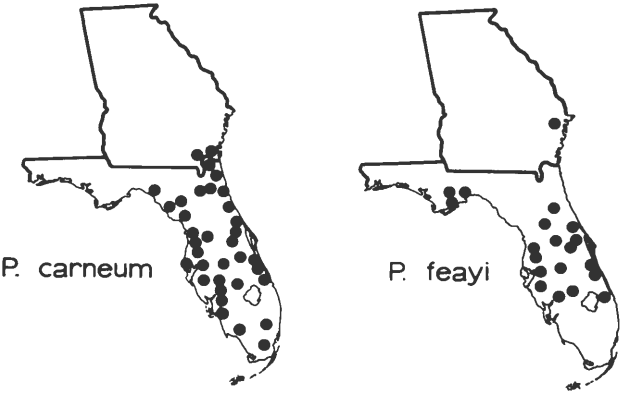
apical petal blades 1.9—3.9 mm long, the claws 0.7—1.7 mm long, less than half the length of the blade. Adroecial tube often equaling the calyx lobes; anthers extended, equaling the length of the petals, yellow-orange at anthesis. Ovary usually bearded or at least slightly pubescent; style bearded proximally from one-third to more than half its length.

Distribution and Phenology

Petalostemon carneum occurs throughout the Florida peninsula and southeastern Georgia. Flowering extends throughout the calendar year but maximum blooming occurs from June through September.

Observations

P. carneum is found in wet, low, undisturbed environments or in low areas where palmettos (Serenoa repens) have become the dominant vegetation. Axillary branching is the rule in this species and often a "pseudocorymb" is formed by axillary spikes that surround the terminal ones. In frost-free areas of its distribution, repeated axillary branching thus allows year-round flowering.



Map 3. Geographic distribution of Petalostemon carneum and P. feayi.

6. PETALOSTEMON FEAYI Chapm. (Map 3, Fig. 9D, 1-3)

Petalostemon feayi Chapm. Fl. S.U.S. ed. 2. 615 (1883). Type in US. (1) (2).

Kuhnistera feayi (Chapm.) Nash. Bull. Torr. Bot. Club 22:149. (1895). Based on Petalostemon feayi Chapm.

Description

Stems numerous, 2—6 dm long arising from a horizontal rootstock or caudex; the central stems erect, the peripheral ones reclining, the whole often forming a hemispherical clump; the lower portions of the stems often with a corky exterior, the upper portions branching, finely striate or smooth; internodes 4—16 mm long. Leaves fascicled, rachis 8—22 mm long, often curved when dried, extension beyond the terminal leaflet pair always less than 0.8 mm; ribs below leaves often lacking or three in number. Leaflets on mature leaves 7—9, usually 7, filiform, involute, often curved when dried, 5—13 mm long and 0.5—1.4 mm broad,

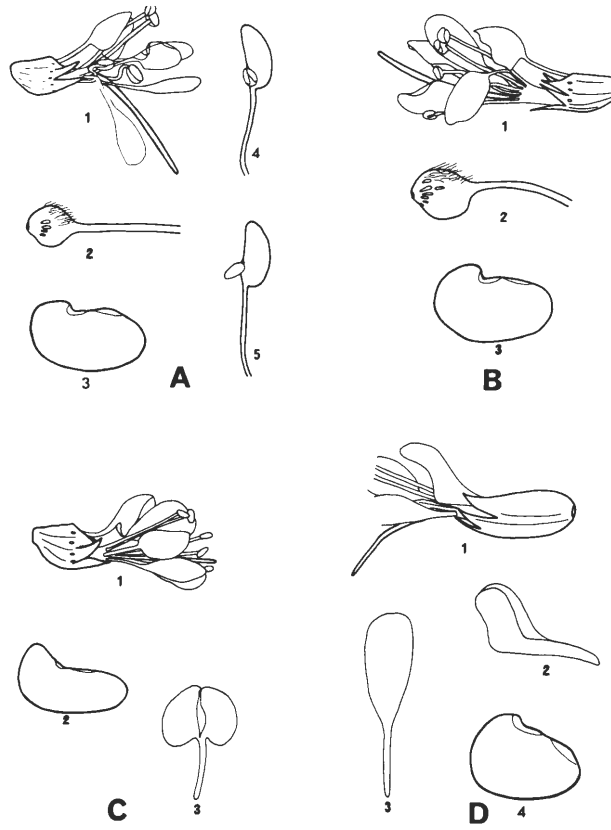


Figure 9. Floral parts of section Candidi (A—C) and Carnei (D). Seeds and ovary drawings x 15, other drawings x 5.
A. P. candidum. 1. lateral view of flower. 2. ovary. 3. seed. 4 and 5. two views of a teratological stamen-petal. The teratology is bilateral—exactly one-half petal, one-half stamen.

B. P. occidentale. 1. lateral view of flower. 2. ovary. 3. seed.

C. P. multiflorum. 1. lateral view of flower. 2. seed. 3. standard—slightly folded at the center of the blade due to the concave nature of the lamina.

D. P. feayi and P. carneum. 1. lateral view of the flower of P. feayi. 2. standard of P. feayi. 3. apical petal of P. feayi. 4. seed of P. carneum.

usually ten times as long as broad. Peduncles 10—80 mm long, usually lacking glands at the apex; sterile peduncular bracts 0.8—3.2 mm in length. Spikes globose, 6—11 mm long and 7—10 mm wide, the lower flowers declined. Bracts shorter than the calyx tubes, narrowly lanceolate, strongly keeled, flanked at the base by a pair of narrowly lanceolate bracteoles. Calyx tubular, slightly gibbous dorsally, glabrous except for a slight ciliation on the inner surfaces of the lobes, 3.2—4.5 mm long, the tube 2.5—3.5 mm long and the ventral lobe 0.7—1.4 mm long. Corolla pink, rarely white; the standard wider than the apical petals, orbicular, 1.4—2.8 mm wide, the claw 3—4 times as thick as the apical petal claws; the blades of the apical petals 2.2—3.6 mm long, the claws 0.9—1.8 mm long, about half the length of the blade. Androecial tube almost always exserted beyond the calyx lobes, the anthers exserted beyond the apices of the petals, orange at anthesis. Ovary globular, glabrous, the style lightly pubescent proximally to half its length, occasionally glabrous.

Distribution and Phenology

Restricted to the white, dry sands of high pine woods of central Florida and southeastern Georgia. Flowering time may extend from February to November, but most plants flower from mid-July to mid-September.

B. SCARIOSI

Distinguishing Characteristics

Stems prostrate, glabrous, covered with reddish-brown, spherical glands; leaflets glabrous, cuneate-obovate; spikes subsessile, becoming lax in fruit; bracts broad and glabrous with scarious and ciliate margins, early deciduous; paired bracteoles present; calyx glabrous except for ciliate lobes, prominently glandular between the calyx ribs, the tube slit dorsally to over 1/3 its length; corolla rose-purple, standard broad-cordate.

7. PETALOSTEMON SCARIOSUM (Wats.) Comb. nov. (Map 4).

Petalostemon scariosum (Wats.) Wemple. Based on Dalea scariosa Wats.

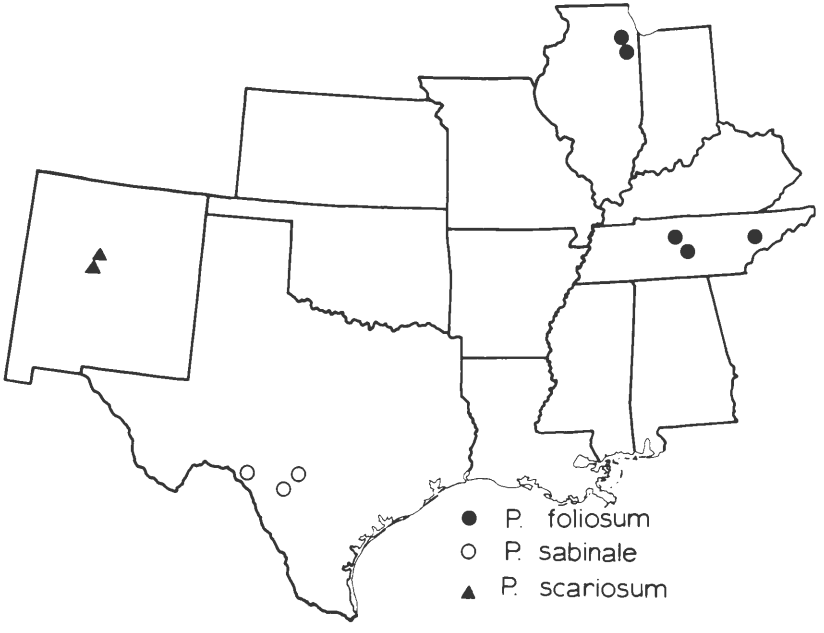
Dalea scariosa Wats. Proc. Am. Acad. 17:369. (1881). Fragments of type in NY. (2) (3).

Petalostemon prostratum Woot. and Standl. Contr. U. S. Nat. Herb. 16:138. (1913). Type in US. (1) (2).

Nomenclature and observations

I have studied the type specimen of P. prostratum (Winnie Howard 17 Albuquerque, New Mexico, 1900) and two other collections from the same locality (Rusby 6 September 1909; Rusby 8 September 1909). Wooton and Standley (loc. cit.) cite another specimen (Wooton 1 August 1906 Belen, New Mexico). Mr. Rupert Barneby has examined fragments of the type of D. scariosa from the same locality and assures me that the two species are identical (pers. comm. 1966).

P. scariosum is very distinctive but shares many characteristics



Map 4. Geographic distribution of Petalostemon foliosum, P. sabinale and P. scariosum.

with P. foliosum and P. sabinale; viz., glabrous stems, leaves and calyx tubes; paired bracteoles flanking the calyces; deeply, dorsally-slit calyces, and lavender to pink corollas. The calyx glands of P. scariosum are similar in size, shape and color to those of P. sabinale. All three species are restricted endemics, although widely separated geographically (Map 4).

P. scariosum differs from the above-mentioned two species in several features, among them: 1) prostrate growth habit; 2) lower leaflet number and obovate leaflets; 3) wide bracts with prominent, scarious margins; 4) suborbicular, prominently lobed standard with a narrow claw; and 5) an elliptically shaped ovary. Therefore, I have not included P. scariosum in the Foliosi. Probably it is related to that group, but not to the same degree that P. foliosum and P. sabinale seem associated.

In the description of the species, the author state the stamen number to be 6. In all flowers that I have examined, the stamen number was 5.

Description

Stems prostrate, 2–6 dm long, round at the base becoming striate toward the apex, straw-colored, glabrous, covered with reddish-brown, spherical glands. Stipules subulate, 2.5 mm long or less, often curved. Leaves glabrous, solitary; leaflets 7-0 (11), inserted in the distal half of the rachis, 6 mm long, 3 mm wide, cuneate-obovate, finely gland-dotted below. Spikes subsessile, 35–90 mm long, 8–9 mm wide, becoming lax in fruit. Bracts glabrous, margins scarious, ciliate, 2.5 mm

broad, precocious, exceeding the calyx lobes in bud, equaling them immediately before anthesis, then deciduous, leaving a prominent heel on the glabrous rachis. Paired, pubescent bracteoles flank the calyx, 1.3 mm long. Calyx tube glabrous, 3.2 mm long, slightly 10-ribbed, with 3-7 protuberant, yellow, pellucid glands lying between the ribs, each gland 0.2-0.3 mm long and 0.1 mm wide; tube slit dorsally to over 1/3 its length, the margin of the slit ciliate; lobes lanceolate, short-ciliate at the margins and on the inner surfaces, the ventral lobe 1.3 mm long. Corolla rose-purple; standard suborbicular, strongly lobed at the base, 4 mm broad, 2.8 mm long; the apical petals 3.5-3.7 mm long, 1.2-2.0 mm broad, the claws 0.7 mm long. Androecial tube not exserted beyond the calyx lobes at anthesis. Ovary 1.8 mm long, 1 mm in diameter, slightly ciliate on the distal portion; style ciliate dorsally only at its proximal end, 8 mm long. Pod not exserted beyond the calyx lobes, slightly ciliate at distal end.

Distribution and phenology

Albuquerque and Belen, New Mexico. Known only from these two locations in Bernallilo and Valencia counties. Flowering time is August to September.

C. CANDIDI

Distinguishing characteristics

Stems glabrous; paired bracteoles, arising from the calyx attachment point on the rachis flanking each calyx; calyx not inflated, + strongly 10-ribbed, glabrous to slightly pubescent, the tube white, the lobes green with prominent glands at their base between the calyx nerves; corolla white, the standard strongly lobed basally and the claw the same diameter as the apical petal claws; ovary with characteristic teardrop-shaped glands on the proximal lateral surfaces.

Distribution and ecology

Wide ranging through the tall grass prairies of the central United States, southern Canada, across the short grass plains to the Rocky Mountains and south to Arizona, northern Mexico and Texas. Seemingly adapted to a wide range of soil types; calcareous prairie soils, rocky limestone soils, clays and sands.

P. candidus, occupying the tall grass prairies of the central United States and Canada, is gradually replaced to the west by P. occidentale and to the south by P. multiflorum. Ecological sympatry occurs, however, only between P. candidum and P. multiflorum. All three species are interfertile, but allopatry and spatial separation of populations are probably important factors limiting hybridization. Of the three, P. multiflorum is distinctive and easily recognized, whereas there has been little agreement among botanists regarding the characteristics of the other species. Isely and Welsh (1960) reviewed the controversy in detail, illustrating how, with multiple characteristics, the two species may be delimited. The sork is summarized by Isely (1962).

Key to the Species

1. Leaflets 9—13 (5 on depauperate specimens), uniform over the entire stem; spikes globose to ovoid, less than 1.5 cm long, entire inflorescence corymbose; bracts shorter than the calyx tube in bud and scarcely exceeding the tube at anthesis. 8. P. multiflorum

1. Leaflets 5—9; lower leaves often with larger leaflets than upper ones; spikes cylindrical, usually exceeding 1.5 cm, not corymbosely arranged; bracts exceeding calyx lobes in bud equaling or exceeding them at anthesis.

   2. Rachis elongating in fruit, separating calyces; calyx usually finely puberulous, strongly 10-ribbed. 9. P. occidentale

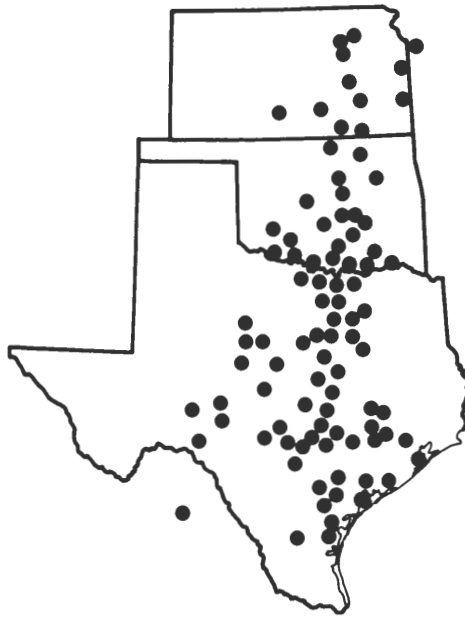
   2. Rachis not elongated, calyces remaining close together even in fruit; calyx glabrous, 10-ribbed but with rounded ridges. 10. P. candidum

8. PETALOSTEMON MULTIFLORUM Nutt. (Map 5, Fig. 9C)

Petalostemon multiflorum Nutt. Jour. Acad. Nat. Sci. Phils. 7:92-93. (1834). Type in PH. (1) (2).
Kuhnistera multiflora (Nutt.) Heller. Mem. Torr. Bot. Club 5:197. (1894). Based on P. multiflorum Nutt.
Kuhnistera candida multiflora (Nutt.) Rydb. Cont. U.S. Nat. Herb. 3:154. (1895). Based on P. multiflorum Nutt.

Description

Plants with coarse, black root system terminating in a woody caudex, occasionally with short rhizomes. Stems many, 3—8 dm long, the central ones erect, the lateral ones almost horizontal often giving a hemispherical appearance to the entire plant; stems glabrous, round when fresh, drying striate above, pale straw color with prominent yellow to red glands; much branched, especially in the upper half of the stem, the uppermost flowering branches usually leafless. Stipules lance-subulate, 1-2 mm long, chartaceous, usually fugacious. Mature leaf rachis 5-15 (25) mm long, never extended beyond the terminal pair of leaflets more than 0.5 mm. Leaflets (5) 7-13, linear-oblong or linear-oblanceolate, often obtuse or mucronate, 6-14 mm long and 2-13 mm wide; prominently gland-dotted only on the lower surface. Flowers disposed in numerous, short, usually globose spikes, 8-12 (25) mm long and 8-10 mm thick, terminating the many upper branches of each main stem. Spike subtended by a whorl of sterile bracts that persists even after fruits fall from the rachis; fertile bracts never exceed the calyx lobes in early bud and are usually shorter than the calyx tube at anthesis, 2.0-2.4 mm long, early deciduous, leaving a prominent "heel" on the rachis. Lance-subulate, ciliate, bracteoles arose laterally and abaxially from the calyx attachment point on the rachis in close proximity to the "heel," 0.1 mm wide at the base, 1.4-1.8 mm long. Calyx tube white, the base suffused with pink, drying straw-colored and strongly 10-ribbed, 2.2-2.6 mm long, 1.6-2.0 mm high; lobes green, deltoid, ciliate on margins, 1.0-1.4 mm long, terminating in a gland; prominent bronze glands between ribs at the



Map 5. Geographic distribution of Petalostemon multiflorum.

base of the lobes. Corolla white, persistent, the standard suborbicular, deeply lobed at the base, 3 mm broad, 2.0-2.8 mm long, the claw 3 mm long; apical petals oblong, 2.2-2.8 mm long, 1.4-1.8 mm broad, the claw 1.3-1.6 mm long. Androecial tube equaling the calyx lobes at anthesis; filaments white; anthers pale yellow, slightly exserted beyond petals. Ovary 1.3 mm long, 0.7-0.8 mm in diameter, slightly ciliate dorsally, otherwise completely glabrous; 4-6 teardrop-shaped protuberant glands are located proximally on the sides of the ovary, the largest above, the remainder decreasing in size below; pellucid when fresh, drying bronze: style glabrous, inserted on the carpel axis, equaling or slightly exceeding the anthers at anthesis. Pod exserted from calyx in fruit, the beak directed upward from the calyx axis. All parts of the plant producing a pungent odor when crushed.

Distribution and phenology

Eastern Kansas south through central Oklahoma, central and central-eastern Taxas; one collection in Chihuahua, Mexico. Limited to relatively dry, rocky prairies. Flowering begins in mid-May for the south Texas populations, mid-June for those in Oklahoma and mid-July for those in Kansas, concluding in early August.

Observations

This species is usually readily distinguished from P. candidum and P. occidentale by the possession of many globose spikes arranged in a corymbose manner and uniform leaves with 9-13 leaflets. Geographically, the range overlaps both with P. candidum and P. occidentale, but, from

my field experience, ecological sympatry occurs only with P. candidum. Although I have never seen these species growing in close proximity, there is evidence indicating occasional hybridization between the two. The putative hybrids possess elongated spikes and bracts exceeding the calyx tubes, sometimes equaling the lobes at anthesis. The elongate spikes are terminal, whereas, the lateral spikes (those producing the corymbose pattern, characteristic of P. multiflorum) are often more globose. Two such collections are from the zone of sympatry: Wemple 396, Cotton Co., Oklahoma, (ISC); and Sizemore 270, Osage Co., Oklahoma (OKLA). In both, spikes up to 25 mm long are common. These characteristics are matched by hybrids between P. candidum and P. occidentale I have synthesized in the greenhouse.

9. PETALOSTEMON OCCIDENTALE (Gray ex Heller) Fernald (Map 6, Fig. 9B).

Petalostemum occidentale (Gray ex Heller) Fernald. Rhodora 39:28. (1937). Based on Kuhnistera occidentalis Heller.

? Petalostemum virgatum Nees von Esenbeck in Wied-Neuw. Reise Nord-Am. 2:432-433. (1840). (2).

Petalostemon gracile Gray. Mem. Amer. Acad. II 4:33. (1848). not P. gracile Nutt. (1) (2).

Petalostemon gracile var. oligophyllum Torr. in Emory, Notes Mil. Recon. Ft. Leavenworth—San Diego. 139. (1849). Type in NY. (2).

Kuhnistera occidentalis Gray ex Heller. Trans. N.Y. Acad. Sci. 14: 33-34. (1894). Based on "Petalostemon candidus var. occidentalis Gray," unpublished name on Pringle labels. (1) (2).

Kuhnistera candida occidentalis Rydb. Contrib. U.S. Nat. Herb. 3:154. (1895). Type material in NY. (1) (2).

Kuhnistera candida diffusa Rydb. Fl. Neb. 59; (1895). Type material in NY. (1) (2).

Kuhnistera oligophylla (Torr.) Heller. Bull. Torr. Bot. Club 23:122-123. (1896). Based on P. gracile var. oligophyllum. Torr. in Emory.

Petalostemon oligophyllum (Torr.) Rydb. Mem. N.Y. Bot. Gard. 1:237-238. (1900). Based on P. gracile var. oligophyllum. Torr. in Emory.

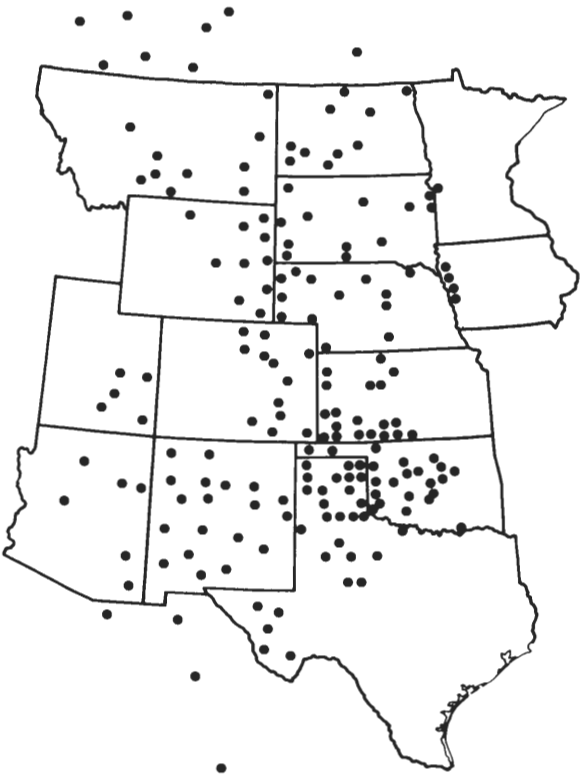
Petalostemon truncatus Rydb. Fl. N. Am. 24:124-125. (1919-1920). Type in NY. (1) (2).

Petalostemon sonorae Rydb. Fl. N. Am. 24:125. (1919-1920). Type in NY. (1) (2).

Petalostemon candidum var. oligophyllum (Torr.) Hermann. Jour. Wash. Acad. Sci. 38:237. (1948). Based on P. gracile var. oligophyllum. Torr. in Emory.

Nomenclature

Except for the unverified virgatum (discussed later) the epithet oligophyllum is the oldest spplied to the taxon. It was not, however, elevated to the species level until two years after occidentalis was proposed, thereby losing priority. K. occidentale Gray ex Heller is based on an unpublished Asa Gray name appearing on Pringle's labels, P. candidus var. occidentalis. Fernald, making the combination, Petalostemon occidentale, says:



Map 6. Geographic distribution of Petalostemon occidentale.

> . . ., Heller definitely stated that he was deriving the name from one used on herbarium-sheets but unpublished by Gray. It seems proper, then to cite Gray as the originator of the name.

His combination was published as Petalostemon occidentale (Gray) Fernald. According to the current rules, a full citation of the name would be, P. occidentale (Gray ex Heller) Fernald; if the author citation is shortened, it becomes (Heller) Fernald.

Since neither Heller nor Fernald designated a type specimen, I have selected as a lectotype, a C.G. Pringle collection labeled, "Petalostemon candidus Michx., var. occidentalis, Gray. Mesas around the Mustang Mts. 26 June 1884," (US 24508).

Petalostemon gracile Gray is Fendler No. 135 from Plantae Fernlerianae (Gray 1849). One of this collection is at MO, and it is clearly P. occidentale. I have not seen the type of P. gracile var. oligophyllum Torr. in Emory, but according to Heller (1896):

> The type, but unnamed, is in the herbarium of Columbia University.

> On a small slip of paper pasted upon the sheet is recorded in Torrey's hand "Emory, Sept. 28th, 1846. Valley of Del Norte."

Heller continues by commenting that, according to the journal, this collection was made near Albuquerque, New Mexico. The Rydberg trinomial, K. candida occidentalis represents the first attempt to merge P. candidum, P. occidentale and P. multiflorum into a single species with three varieties. He cites no synonymy but lists 19 representative collections, all in NY. His publication of P. diffusa followed later the same year and was said to be like K. candida occidentalis, "but prostrate, decumbent, or diffuse . . . Petalostemon gracilis Gray in Pl. Fendl. may belong here. Deuel Co., Rydberg 58." I have examined four collections labeled Rydberg 58, only two of which have labels indicating the same location, although all are from Deuel Co. Three are referrable to P. occidentale, but the fourth is definitely P. candidum, the most western collection of that taxon. Rydberg does not include the epithet diffusa in Flora of North America (1919-1920).

P. truncatus Rydb. is based on Palmer 284, NY, collected at Tepehuanes, Durango. I have examined the type, an isotype at US, as well as three sheets annotated by Rydberg reassigning them to this taxon. The definitive characteristic of this species, according to Rydberg, is the presence of petals truncate at the base of the lamina. Had he examined petals from specimens collected throughout the range of P. occidentale he would have found that truncate petals are not an exclusive characteristic of plants from northern Mexico. With regard to petal shape, I sampled specimens at random from this taxon (Fig. 7). The least truncate petals seen were from one of Rydberg's own collections (Rydberg 59, Deuel Co., Nebraska). The type location of P. truncatus is the southernmost spot on the distribution map.

P. sonorae, another Rydberg name, is based on a Schott collection made during the Emory, Mexican Boundary Survey, No. 241. The location is shown on the distribution map as the most western Mexican collection. According to Rydberg, it is characterized by having: 1) scattered leaves, 2) long acuminate bracts exceeding the calyces in bud and in fruit, and 3) compact spikes. I have examined the type and an isotype at NY and find tham both well within the range of variability of P. occidentale. Both specimens have lost most of their upper leaves; the lower leaves, usually more scattered and larger, remain. The weak midrib, characteristic of P. occidentale, is clearly seen. The bracts barely exceed the calyx lobes in late bud and are usually lost before anthesis. There is evidence of some, although not excessive rachis expansion. T. H. Kearney recognized this taxon and five Arizona specimens are so labeled in US. On one (Peebles 5329) is the comment, "Related to P. oligophyllus and perhaps not sufficiently distinct. (THK)."

Petalostemon virgatum was included in the synonymy of P. candidum by Rydberg (1919-1920). Perhaps this placement was motivated by the title of Nees von Esenbeck's paper, "Botany of Missouri." From the description in the original publication, the specimen would seem to be P. occidentale. Particularly indicative of this is, "calyx . . . glaber aut pubescentia laxissima minutissimaque conspersus, compressus, . . ." I have been unable to locate the Nees herbarium and thus have not seen a

type specimen for this name. If the description is verified by a type, the epithet has clear priority over all other names and should be adopted.

Description

Stems several, branching above, decumbent to erect, glabrous, 4-8 dm long; coarsely striate, often drying a glaucous, pale green. Stipules 3.0-4.5 mm long, drying brown, fragile. Mature leaf rachis, 10-20 (30) mm long bearing 5-7 (9) glabrous, gland dotted, elliptical-oblong or oblanceolate, often emarginate, involute leaflets, 5-10 (15) mm long, 2-4 (5) mm wide; often with larger leaflets at the base of the plant; the leaflet midrib is usually not prominent on the lower surface. Flowers disposed in a columnar spike which becomes lax in fruit, 6-8 mm wide and up to 70 mm long; occasionally with a few short, sterile bracts at varying distances below the spike. Fertile bracts exceeding the calyx lobes in bud, deciduous prior to anthesis, usually leaving a short "heel" on the rachis. Bracteoles filiform, 1-2 mm long, slightly ciliate, inserted beside calyx attachment point on rachis, quite separate from the bract "heel." Calyx tube white, strongly 10-ribbed drying sharp-ribbed, not round-furrowed as in P. candidum; usually ± pubescent between ribs, 2.3-2.9 mm long, 1.6-2.0 mm in diameter; lobes green, deltoid-lanceolate, ciliate at margins, the ventral lobe 1.0-1.3 mm long; prominent glands at base of lobes between ribs of calyx tube, drying bronze. Corolla white, standard 2.6-3.3 mm broad, 1.8-2.2 mm long, lobed at base, the claw 3.0-3.5 mm long; apical petals elliptical-oblong, 2.5-3.0 mm long, 0.9-1.4 mm wide, the claw 1.1-1.3 mm long. Standard tube exserted beyond calyx lobes at anthesis; anthers not extended to petal tips, pale yellow, drying yellow-brown. Ovary glabrous save for ciliate fringe on dorsal surface, 1.3-1.7 mm long, 0.8-1.0 mm in diameter; style glabrous, inserted slightly above carpel axis, 8-10 mm long, exceeding the petal tips. In fruit, the pod exceeding calyx, the beak directed upward, between dorso-lateral lobes.

Distribution and phenology

Southern Alberta, Saskatchewan and southwestern Manitobe, south throughout the short grass plains to western Texas, Durango, Arizona and southeastern Utah. Western representatives are always found at high altitudes, e.g., New Mexico, 6000 ft.+, Arizona, 6000 ft.+, Colorado, 4500 ft.+. Adventive to the east in particularly xeric environments; e.g., the loess bluffs along the Missouri River at the Iowa-Nebraska border. Ubiquitous throughout its range except for the lower elevations to the west. It is found in sands, limestones and clays. Its aggressiveness is shown by its ability to colonize road cuts. Blooming time is from late May until early August, blooming first in the southern part of its range.

Observations

Petalostemon occidentale can be distinguished from P. candidum on the basis of multiple characteristics as previously discussed. Gross, visual characters, easily seen in the field are: 1) a more diffuse, spreading growth pattern, 2) a lower leaflet number with smaller leaflets, and 3) a spike that elongates following anthesis. P. occidentale is not as homogeneous a species as P. candidum. Variation appears chiefly in leaflet size and shape. Throughout most of its range, the leaflets are

small. If large leaflets are present, they are restricted to the lower portions of the stems; however, in Colorado and Montana there are specimens possessing only large leaflets. This condition mimics the leaflet size found in P. candidum and has been partly responsible for the identification of some of the Rocky Mountain material as P. candidum. In the same general area where the broad leaflet forms are found, the more typical plants have also been collected. Variation is also seen in calyx pubescence. Many of the western specimens lack pubescence entirely. This is particularly evident in those from the southwest. The ribs of the calyx nerves are also less prominent in the western specimens and some have rather pronounced bract "heels." In short, many of the western specimens seem more "candidum-like" than those found in the zone of overlap of the two species. Superficially one might hypothesize that the difference in morphology of the eastern species in the sympatric region might be a reflection of a genetic barrier, operating to prevent introgression with P. candidum. Such a situation, called a "reverse cline" (Creed et al. 1969; Harper et al. 1961) has been postulated in the study of animal species. Such a hypothesis is not warranted in this instance, because the two species, even when geographically sympatric, are not at all ecologically sympatric. P. occidentale is restricted to xeric habitats while P. candidum grows in the richer more mesic prairie habitats. A better explanation for the greater variability of P. occidentale as compared with P. candidum might be varying environments over the range in which the former species grows. As indicated, all the western populations of P. occidentale are high altitude forms. Undoubtedly these habitats have acted as selectors for certain phenotypes different from those at the lower elevations. The variance exhibited by P. occidentale is probably a reflection of a basic plasticity within its genetic makeup.

10. PETALOSTEMON CANDIDUM Michx. (Map 7, Figs. 9A; 12B)

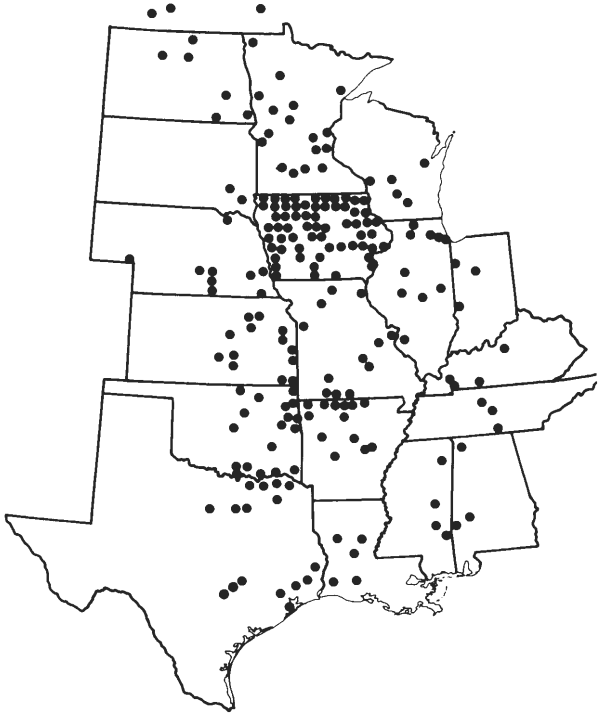
Petalostemum candidum Michx. Fl. Bor. Am. 2:49, tab. 37, 1. (1803). Type material at P. (1)(2).
Dalea candida Michx. ex Willd. Sp. Fl. 3:1337. (1802).
Psoralea candida (Michx.) Poir. In: Lam. Encycl. Meth. 5:694. (1804). Based on Dalea candida Willd.
Kuhnistera candida (Michx.) Kuntze. Rev. Gen. Pl. 1:192. Based on Petalostemon candidum Michx.

Nomenclature

Many authors cite P. candidum (Willd.) Michx. on the basis of the earlier publication of Willdenow's Species Plantarum. As Isely (1962) points out (p. 120):

> . . . since Michaux did not cite Willdenow (the contrary is in fact the case), his epithet would seem to be most properly considered a new name rather than a combination. The correct citation should be P. candidum Michx.

It is probably that this species was introduced into Europe at the same time as P. purpureum. Both grew together in Illinois (the stated locale of the Michaux collections) and seeds of both were undoubtedly gathered



Map 7. Geographic distribution of Petalostemon candidum.

and returned to Europe. In support of this hypothesis is a specimen from the Herbarier de Ventenat (G) which is labeled, "ex H. Cels." It was from a plant growing in the gardens of M. Cells that Ventenat described P. purpureum and it is likely that cultivation of P. candidum was attempted there also. A plausible explanation for Ventenat not including a report of both species is that P. purpureum flowers more readily from seed than does P. candidum. Seedlings of the latter species rarely flower the first year while those of P. purpureum flower during their first growing season.

Description

Stems few, arising from a woody caudex, 3-10 dm long, usually erect, moderately branching above; glabrous, striate, the protruding ribs drying white or pale green. Stipules white when fresh, drying straw-colored, persistent, subulate, 4-7 mm long. Leaves remote, glabrous, slightly fascicled, usually with not more than three small, inconspicuous, axillary leaves; rachis green, winged, often expanded just proximal to the petiolules forming a tubercle, always extended 1.0-1.5 mm beyond the terminal pair of leaflets; leaflets 5-9, elliptical to oblanceolate, 10-30 mm long, 2.5-7.0 mm wide, the lower surface dotted with small glands and possessing a prominent midrib when dry which usually terminates in a mucro. Peduncles 5-10 cm long, interrupted by prominent

sterile bracts, 1-2 cm long, scattered below the spikes. Flowers in compact, nonexpanding spikes, 1-8 cm long, 7-9 mm wide, sweetclover scented. Bracts precodious and persistent, far exceeding the calyx lobes in bud, slightly exceeding them at anthesis; body 2.0 mm long, ciliate margined, expanded and prominently glandular below the acumen; acumen subulate, often curved abaxially, abscission leaving a prominent "heel" on the rachis; paired, subulate, ciliate bracteoles, 1.5 mm long, flank the base of each flower. Calyx tube neither strongly 10-ribbed nor pubescent, usually drying with smoothly rounded longitudinal furrows; white, suffused with pink at the base when fresh, drying to a pale straw color, 2.0-2.5 mm long, 1.7-2.0 mm in diameter; lobes green, ciliate on margins, lanceolate, the ventro-lateral lobes often directed upward overlapping dorsal-lateral lobes; ventral lobe, 1.4-1.6 mm long; a pair of prominent glands, drying yellow to bronze, immediately below each lobe between the calys bundles. Corolla white; standard lamina strongly concave and lobed basally, 2.2-2.5 mm broad, 2.0 mm long, the claw 3.0-3.3 mm long; apical petals oblong-oblanceolate, 2.2-3.3 mm long, 1.2-1.5 mm wide, slightly cuneate at base, the claw 1.8-2.2 mm long. Androecial tube not exserted beyond apex of calyx lobe, 3.5 mm long; filaments equaling or slightly exceeding the petal tips at anthesis; anthers pale yellow. Ovary globose, glabrous except for tuft of cilia on dorsal surface, 0.7-1.2 mm long, 0.6-1.1 mm in diameter; teardrop-shaped glands prominent on proximal-lateral surfaces, smaller toward ventral side of ovary, drying dark colored; style exserted beyond petal tips soon after anthesis, 7.0 mm long. Pods exserted from calyx, the beak angled upward between dorsolateral lobes, prominently glandular.

Distribution and phenology

A widespread species from southern Manitobe and Saskatchewan, eastern Dakotas, Minnesota and Wisconsin; south, to eastern Texas, Louisiana, Mississippi and Alabama. Occupying primarily prairie habitats, open woodlands and glades, occasionally adventive along roadsides. Replaced in the High Plains to the west by P. occidentale. P. candidum is ecologically sympatric with P. purpureum throughout most of its range; the two are frequently present on prairie remnants. Anthesis time is from mid-May to late July, flowering proceeding south to north.

Observations

Isely and Welsh (1950) clarified the species status of P. candidum and P. occidentale. As they pointed out, the two are quite distinct when multiple characteristics are used for differentiation. My studies have corroborated their findings; however, I find no indication of any introgression in the sympatric zone of the two species. Indeed, eastern specimens of P. occidentale (those sympatric with P. candidum) are more readily separated from P. candidum than are those collected farther west. Some of the western forms have many characteristics of P. candidum (e.g., broader leaflets and more glabrous calyces) but their habitats—usually 5000 ft. elevation and above—are probably in part responsible for the apparent morphological convergence toward P. candidum. In the sympatric zone, the two species are not ecologically congruent. P. occidentale is always found in the more zeric habitats, whereas P. candidum is found in the mesic areas of rich prairie soil.

P. candidum and P. multiflorum are geographically sympatric over a great part of the range of the latter species. Habitat preference is almost always identical and occasional interbreeding evidently takes place. The rare, putative hybrids found in herbarium collections match those I have synthesized in the greenhouse.

Despite the few intermediates resulting from hybridization, P. candidum is morphologically consistent for such a wide ranging species. It can readily be recognized by its upright growth habit, relatively few leaves but large leaflets, long, nonexpanding, columnar spike with precocious and persistent bracts. The main exceptions are to be found in the Southeast, where habitats of heavy clay soils and glade environments have evidently acted as selective forces to shape a more decumbent-prostrate stem and in general, a smaller plant. Despite the reduced size and growth habit of these plants, their floral characteristics match those in the other parts of the range.

D. FOLIOSI

Distinguishing characteristics

Plants completely glabrous. Stems round below, becoming striate above. Leaves mostly solitary; leaflets 13-27. Spikes becoming lax at anthesis. Bracts lanceolate, scarcely expanded proximally, short ciliate on margins only, otherwise glabrous, far exceeding the calyx lobes in bud but early deciduous. Paired bracteoles present, flanking the base of the calyx. Calyx tube glabrous, 10-ribbed, gibbous dorsally and slit to almost half its length, slit margins ciliate as are the lobe margins. Corolla pale lavender to rose, the standard broad, rounded-deltoid, its claw much thicker than the claws of the apical petals.

Distribution and ecology

Both species are rare and evidently restricted to specialized habitats in the Tennessee Basin and south central Texas. The northern species perhaps currently restricted to limestone glades; the southern species to "exposed rocks" and "limestone clefts" according to herbarium labels.

Observations

These two species, although widely separated geographically, share many of the same characteristics, presumably indicating that they are closely related. Since both are highly restricted and rare, they possibly represent relict populations of formerly more widely spread taxa. They are both so distinct from the other species or groups of species of Petalostemon that it is unlikely they arose as a result of relatively recent hybridization between more wide-ranging species and persisted because of their ability to survive in specialized habitats. Possible distant relationship with P. scariosum, a rare endemic from New Mexico, is discussed under that species. Further collecting may possibly indicate that both are more widespread than currently known.

Key to the Species

1. Leaflets 20-29, elliptical; peduncles shorter than 3 cm; spikes compact; calyx tube not prominently gland-dotted; ovary covered with prominent, protuberant, spherical glands; Illinois and Tennessee 11. P. foliosum

1. Leaflets 7-17, linear; peduncles 6-12 mm; spikes lax; calyx tube with numerous glands between ribs; ovary not glandular; Texas 12. P. sabinale

11. PETALOSTEMON FOLIOSUM Gray (Map 4, Fig. 10D)

Petalostemon foliosus Gray. Proc. Amer. Acad. 7:336. (1868). Type in GH. (1)(2).
Kuhnistera foliosa (Gray) Kuntze. Rev. Gen. Pl. 1:192. (1891). Based on Petalostemon foliosus Gray.

Description

Stems several, 3-8 dm long, branching above, smooth, glabrous, round at the base but becoming striate immediately below the spike. Internodes 1.0-1.5 cm long. Stipules subulate, 3-5 mm long, persistent, becoming sinuous when dried. Leaves 3.5-4.5 cm long, initially solitary at nodes ultimately becoming fascicled on older stems; leaflets 20-29, evenly spaced along rachis, not always paired; petiolules 0.5 mm long with a prominent gland on lower surface of the rachis at the point of insertion; blade 6-10 mm long, 2.5-3.5 mm wide, elliptical to elliptic-obovate, mucronate, finely gland-dotted; midrib very prominent on the ventral surface. Peduncles short, 1.5-2.5 cm, bearing scattered sterile bracts, 5-16 mm long. Spikes clustered, moderately compressed, cylindrical, 8-10 mm broad, 25-50 mm long. Bracts subulate, expanded in the center, about 5 mm long, far exceeding the calyx lobes in bud, becoming chartaceous and falling soon after anthesis. Subulate bracteoles flank the calyx, 0.5-1.0 mm in length. Calys tube white, thin walled, 3.5-3.8 mm long, gibbous distally, narrowing proximally, slit dorsally to almost half its length, slightly oblique, laterally ribbed; rachis attachment point below the longitudinal axis of the tube; lobes deltoid, green, appressed pubescent on inner surface and margins, the ventral lobe 2.0 mm long. Corolla pale purple, the petals widely reflexed; standard ovate-emarginate, 3 mm wide, 2.5 mm long; claw 4 mm long, 0.3 mm thick (over twice as thick as claws of apical petals); apical petals narrow, 2.7 mm long, 0.8 mm wide, slightly truncate anteriorly, cuneate at base, the claw 0.8 mm long. Staminal tube 3.6 mm long, shorter than calyx lobes; filaments 4.0 mm long, the anthers bright red-pink before anthesis; pollen orange. Ovary spheroidal, 1.4 mm long, 0.9 mm in diameter, glabrous, covered with protuberant, spherical glands; style glabrous, 5.5 mm long. Pod gland-dotted, exserted slightly from calyx, the anterior portion directed upward between the dorso-lateral lobes.

Distribution and phenology

Known originally from northern Illinois and the Tennessee Basin. It appears now restricted to limestone glades in the latter area. Blooming time is from July to mid-September.

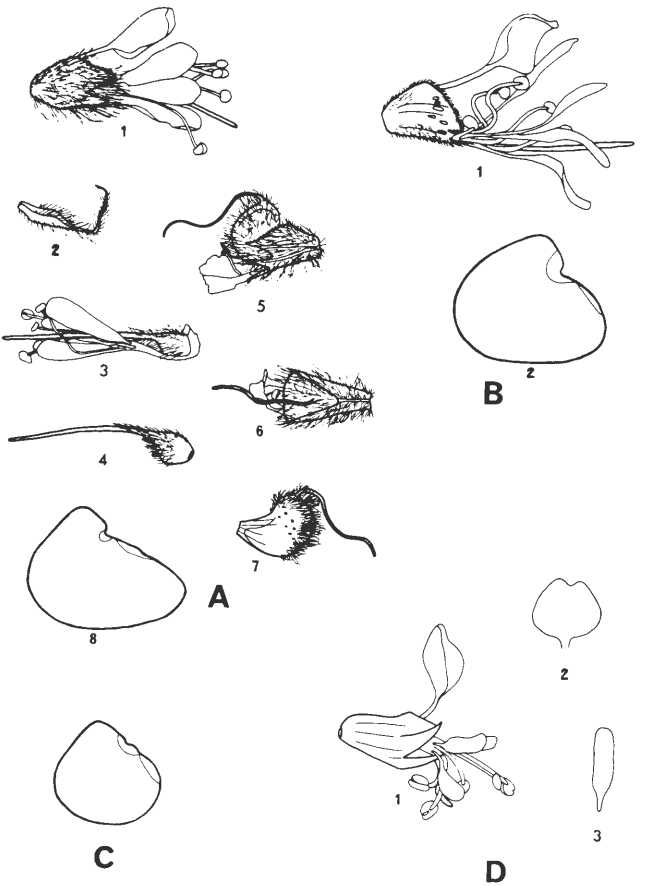


Figure 10. Floral parts and seeds of selected species of sections Villosi, Phleoides, Foliosi and subg. Kuhnistera. Seed drawings x15, other drawings x 5.

A. P. villosum. 1. lateral view of flower. 2. bract. 3. androecium and gynoecium with the standard removed. 4. carpel. 5. mature fruit, lateral view. 6. mature fruit dorsal view. 7. legume. 8. seed.

B. P. microphyllym. 1. lateral view of flower. 2. seed.

C. P. pinnatum ssp. trifoliatum, seed.

D. P. foliosum. 1. lateral view of flower. 2. standard blade. 3. apical petal.

Observations

The type sheet in the Gray Herbarium bears two collections, those of Truesdale (year) 1867, Kane Co., Illinois and Hatch (year) 1854, Nashville, Tennessee. Both are cited by Gray. A similar mixed sheet is at MO and a specimen of the Truesdale collection is at NY. There have been no collections from the intervening areas, and few collections of the species have been made in this century. The habitat of the "cedar glades" of the Tennessee Basin has been discussed under P. gattingeri, a species also endemic to these areas. My collection of this taxon (Isely and Wemple 9420) was late in the season and only a few axillary spikes remained in bloom. Seeds were collected and the plants grown and flowered in the Iowa State University greenhouse. They grew well in our prairie loam potting soil and flowered readily. Observations of living plants and fresh flowers facilitated preparation of the above description. As with all other species of Petalostemon cultivated under greenhouse conditions, there appear to be no artifacts induced. Pressed specimens from the greenhouse appeared exactly like those collected in the field.

This taxon is quite distinct from any other. Its possession of many leaflets, long, precocious, subulate bracts, bracteoles and glabrous calyx seem to relate it to P. sabinale (Rydberg, 1919-1920, places them in the same section), but leaflet shape, peduncle length, calyx shape, texture, and glandlessness, as well as a glandular ovary, set P. foliosum apart.

12. PETALOSTEMON SABINALE Wats. (Map 4)

Petalostemon sabinalis Wats. Proc. Am. Acad. 21:448-449. (1886). Type in GH. (1)(2).

Kuhnistera sabinalis (Wats.) Heller. Bull. Torr. Bot. Club 23:124. (1896). Based on Petalostemon sabinalis Wats.

Petalostemon luteolus Wats. ex Heller. Bull. Torr. Bot. Club 23: 122. (1896).

Nomenclature and observations

The epithet luteolus was a tentative name placed in parentheses on the label of the type specimen of P. sabinale by Sereno Watson (loc. cit.). Watson eventually rejected the name and published the species as P. sabinalis. Heller (1896) restored the epithet, in a sense, by commenting:

> Petalostemon luteolus S. Wats., is P. sabinalis S. Wats. Although the name luteolus appears in Patterson's Check-List, it has no foundation, being a label name given to a specimen of P. sabinalis.

The affinities of P. sabinale are decidedly with P. foliosum as first suggested by Rydberg (1919-1920). Turner (1959, p. 165) indicates that it is, "Closely related to P. stanfieldii [P. tenue] and apparently intergrades with that species." I find no evidence to support this view. It is true that the range of the two species is contiguous and that the leaflet number is similar, but all other characteristics are decidedly different—the two are quite remote morphologically.

It is possible that this species is more common than the paucity of collections indicate and could be "rediscovered." The type location, "entrance to Sabinal Canyon," is not readily accessible, but a 1944

collection (Cory 44424, Val Verde Co., Texas) 12 3/4 miles south of Loma Alta, Texas is evidently along a highway. I collected for a day in this area during mid-June 1962, but did not find the species. My efforts were probably too late in the season and perhaps an earlier visit would bring it to light.

Description

Stems many, unbranched, erect, 2-4 dm long, glabrous, slightly glandular, round at the base becoming slightly striate above. Stipules fugacious, 2-4 mm long, subulate, often curved. Lower leaves solitary, the upper ones often with suppressed axillary branch systems; rachis 2.0-2.5 cm long, glabrous, glandular, extended beyond terminal pair of leaflets 0.8-1.5 mm; leaflets (7) 13-15 (17), linear, narrowed at base, 9-13 mm long, 1.5-2.0 mm wide, pale green above, darker green and gland-dotted below. Peduncle glabrous, 6-9 (12) cm long, rarely bearing sterile bracts near the apex. Inflorescence an expanding spike, up to 5 cm long; rachis glabrous to glabrate. Bracts precocious, far exceeding the calyx lobes in bud, deciduous before anthesis, lanceolate, only slightly broadened at the base, short-ciliate on margins; paired, ciliate bracteoles 0.5-1.0 mm in length, flank the calyces. Calyx expanded-tubular, slightly 10-ribbed, 2.2-2.9 mm long, slit dorsally almost half its length, glabrous except for margins of dorsal slit which are short ciliate; tube glandular at base of lobes with numerous, yellow, pellucid, protuberant glands 0.2-0.3 mm long, 0.1 mm wide; lobes ciliate, the ventral lobe 0.8 mm long. Corolla rose to pale lavender (?); the standard rounded-deltoid, 3.0 mm long, 3.5 mm broad, slightly emarginate at apex, the claw 3.5-3.9 mm long, thicker than the claws of the apical petals; apical petals 3.5 mm long, 1.0 mm wide, the claws 1.0 mm long. Androecial tube exserted beyond tips of the lobes, 3.5 mm long; the free filaments 5.3 mm long. Ovary 1.4 mm long, 1.0 mm in diameter, only slightly short-ciliate on dorsal, distal surface; the style 8 mm long. Pod not exceeding calyx lobes but bent upward between dorsal lobes, short ciliate on apical margins.

Distribution and phenology

Known only from five collections in Texas; Bandera, Brewster, Uvalde and Val Verde counties. Apparently blooming in mid-May.

E. PHLEOIDES

Distinguishing characteristics

Stems striate with protuberant, globose glands; leaflets 11-48, glabrous to pubescent, sessile or nearly so; spikes 1.3-6.7 cm long, often becoming sinuous, 5-9 mm wide; bracts linear, exceeding calyx lobes, often deciduous; paired filiform bracteoles present, flanking the calyces; calyx oblique, deeply slit and dorsally gibbous, the lobes very short; corolla white, the standard broad, the apical petals strap-shaped.

Distribution and ecology

Dry sandy areas of south and east Texas and adjacent Oklahoma.

Observations

This section is easily recognized by its white flowers, dorsally gibbous

calyx, numerous leaflets and spherical, protuberant glands, to 1.3 mm in diameter. The glands when ruptured, release a pungent, watery liquid that has a sharp, distinctive odor. P. microphyllum has been in greenhouse cultivation for over 2 years. It thrives and flowers freely when grown in Iowa prairie soil. All attempts at cross-pollination with other species of other sections have been unsuccessful; indicative, as is the morphology, of the distinctiveness of these species within the genus.

The treatment of this section is in large part based upon unpublished investigations of Wesley S. Jackson (1964). Before Jackson's study, Phleoides was conventionally considered to contain three species (Rydberg 1919-1920, Turner 1959), but their distinguishing characters were far from clear. On the basis of analyses of mass collections, as well as field and herbarium studies, Jackson demonstrated the existence of two reasonably distinct taxa. Their diagnostic characteristics are presented in the following key.

Key to the Species

1. Calyx glabrous; leaves (0.7) 1.3-2.3 (3.8) cm wide, leaflets 11-26, usually under 21; peduncles usually possessing sterile bracts. 13. P. phleoides

1. Calyx pubescent; leaves (0.5) 0.6-1.5 (2.0) cm wide, leaflets 15-48, usually over 25; peduncles usually lacking sterile bracts. 14. P. microphyllum

13. PETALOSTEMON PHLEOIDES T. and G. (Map 8)

Petalostemon phleoides T. and G. Fl. N. Am. 1:310. (1838). Type in NY. (1)(2).
Petalostemon aphleoides Young. Fl. Tex. 221. (1873). (2)
Kuhnistera phleoides (T. and G.) Kuntze. Rev. Gen. Pl. 1:192. (1891). Based on Petalostemon phleoides T. and G.
Petalostemon glandulosus Coult. and Fish. Bot. Gaz. 18:229. (1893). Type in US. (1)(2).
Dalea phleoides (T. and G.) Shinners. Field and Lab. 17:83. (1949). Based on Petalostemon phleoides T. and G.
Dalea glandulosa (Coult. and Fish.) Shinners. Field and Lab. 17:83. (1949). Based on Petalostemon glandulosus Coult. and Fish.

Nomenclature and observations

Although Rydberg (1919-1920) and Turner (1959) upheld separation of P. phleoides and P. glandulosum, merger of the two species was first proposed by Heller in 1896 (p. 123). Under Kuhnistera phleoides, he writes:

> A comparison of phleoides and a duplicate type of glandulosus, both of which are in the Columbia University Herbarium, clearly shows them to be identical. The oblique calyx is a marked character of this species.

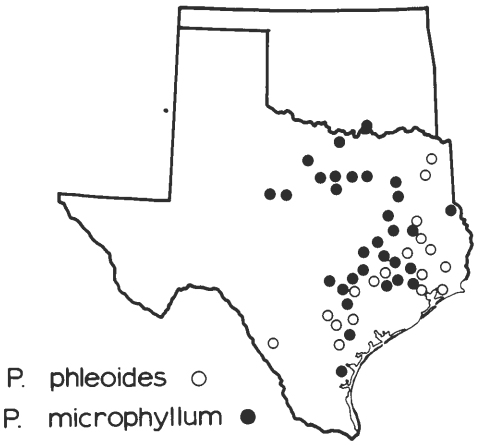
Heller also indicated the general lack of pubescence of K. phleoides in his earlier remarks regarding K. microphylla. Jackson's detailed study of these species corroborates Heller's intuitive approach.

Description

Multiple stems ascending from a rusty to deep red taproot. Stems 2-7 dm long, glabrous to slightly pubescent, striate and glandular. Stipules 2.5-3.5 mm long, pubescent, subulate from a broad base. Leaves 2.1-6.7 cm long, 0.5-3.8 cm wide, glabrous to pubescent; leaflets 11-26, elliptical to obovate, 1.5-2.5 mm long, 0.4-1.0 mm wide. Peduncles 0.1-26.3 cm long, usually with scattered sterile bracts near the apex. Spikes dense, cylindrical, becoming lax and sinuous in fruit, 13-58 mm long, 5-9 mm wide. Bracts glabrate in the southern portion of the range, becoming more pubescent northward, exceeding the calyx lobes in bud, deciduous before anthesis. Bracteoles present, flanking the calyces, 0.6-1.0 mm in length. Calyx glabrous; the tube oblique, 2.2-2.6 mm long, slit more than half its length dorsally, glandular between the nerves; lobes 0.6-0.9 mm long, ciliolate on margins. Corolla white; the standard blade cordate, 2.5-3.5 mm long, 2.5-3.5 mm wide, the claw 3-4 mm long, apical petals linear, 3.0-3.5 mm long, 0.6 mm broad, the claws 2.0 mm long. The staminal tube about 2.7 mm long, the free filaments 2.5-3.5 mm long; anthers orange. Ovary 1.0 mm long, glabrous; the style 5 mm long, proximally pubescent on the upper surface for one-third its length. Pod obliquely obovoid.

Distribution and phenology

Eastern and southern Texas. Primarily confined to deep sands of pine and oak woodlands. Flowering from mid-May to mid-July, reaching a maximum the third week of July.



Map 8. Geographic distribution of Petalostemon phleoides and P. microphyllum.

14. PETALOSTEMON MICROPHYLLUM (T. and G.) Heller (Map 8, Fig. 10B; 12C)

Petalostemon microphyllum (T. and G.) Heller. Bull. Torr. Bot. Club 26:593. (1899). Based on Petalostemon phleoides var. microphyllum T. and G.

Petalostemon phleoides var. microphyllum T. and G. Fl. N. Am. 1:310. (1838). Isotype in US. (1)(2).

Kuhnistera microphylla (T. and G.) Heller. Bull. Torr. Bot. Club 23:122. (1896). Based on Petalostemon phleoides var. microphyllum T. and G.

Dalea drummondiana Shinners. Field and Lab. 17:83. (1949). Based on Petalostemon phleoides var. microphyllum T. and G.

Description

Stems arising from a deep, red taproot, 2-7 dm long, glabrous to pubescent, striate, with protruding, globose glands. Stipules 3-5 mm long, curved. Leaves 1.4-6.0 cm long, 0.5-1.8 cm wide, glabrous to pubescent (densely so on young leaves); leaflets 15-48, elliptical to obovate, sessile or nearly so, 4-7 mm long, 1.5-2.0 mm wide. Peduncles 0.1-22.5 cm long, usually without sterile bracts near the apex. Spikes 5-103 mm long, 5-48 mm wide. Bracts exceeding the calyx in bud, often deciduous, linear to linear-lanceolate, 4-5 mm long, 0.3 mm wide with subulate to subulate-filiform tips, glabrous to pubescent. Paired bracteoles present flanking the calyx, 0.6-0.8 mm long, filiform. Calyx oblique; the tube 3 mm long, slit dorsally to more than half its length, dorsally gibbous; the lobes short, the ventral lobe less than 1.3 mm long, ciliolate on the margins. Corolla white; the standard blade cordate, 2.5-3.0 mm long, 2.5-3.5 mm wide, the claw 3-4 mm long; apical petal blades linear to linear-oblanceolate, 2.5-3.5 mm long, about 0.7 mm wide, the claw 1.5-2.5 mm long. Androecial tube exserted slightly beyond the tips of the calyx lobes. Ovary 1.4 mm long, 0.8 mm in diameter, ciliate on the proximal two-thirds. Pod obliquely obovoid.

Distribution and phenology

Northern and eastern Texas in the deep, dry sands of the Cross Timbers and Prairies, Blackland Prairies, and South Texas Plains vegetational areas (Gould 1962). North to Montague county, south to Nueces county and extending west to Taylor county, Texas. Also from Marshall county, Oklahoma. Flowering from late May to mid-July, reaching a maximum during the second week of June.

Observations

This is a variable species, and Turner (1959) has suggested that two varieties are possibly represented. His conjecture was based on the more glabrous condition of the northern populations. Jackson (1964) confirms Turner's observations but states:

> However, no reasonable cline can be observed. Further, no other morphological features seem to exhibit a north-south bifurcation. Thus at this time Petalostemon microphyllum is considered as one entity though a highly variable one.

Jackson concludes his discussion with this paragraph:

> From both field and herbarium experience, both species of the section are highly variable. Each is probably represented by individual colonies or populations with not much interbreeding from one colony to the next, thus each colony is highly individualistic.

F. VILLOSI

Distinguishing characteristics

Stems arising from a long, red, seldom branched taproot; stems and leaves villous, leaflets (9) 11-19 (21), less than 1.9 cm long; spikes lax, usually 5-12 cm long and less than 1 cm broad; flowers pale lavender, rose to almost white.

Distribution and ecology

Texas, northward to southern Saskatchewan, throughout the Plains area on sandy soil, sandhills and blowouts.

Key to the Species

1. Stems reddish, striate, spreading pubescent; leaves thinly pilose, leaflets 10-15 mm long; not possessing sterile bracts below spikes; standard broad, cordate; east Texas and western Louisiana. 15. P. griseum

1. Stems pale, striations usually concealed by villous investure; leaves densely villous, leaflets 8-11 mm long; sterile bracts straggling down peduncle below spike; standard oblong, truncate or rounded at the base; central or north Texas and northward. 16. P. villosum

15. PETALOSTEMON GRISEUM T. and G. (Map 9)

Petalostemon griseum T. and T. Fl. N. Am. 1:310. (1838). Type in NY. (1)(2).

Kuhnistera grisea (T. and G.) Kuntze. Rev. Gen. Pl. 1:192. (1891). Based on Petalostemon griseum T. and G.

Dalea grisea (T. and G.) Shinners. Field and Lab. 17:84. (1949). Based on Petalostemon griseum T. and G.

Nomenclature and observations

Torrey and Gray cite two collections, "Pine woods near the Sabine River, Dr. Leavenworth! Texas, Drummond!". Both are mounted on 1 sheet at NY. The Leavenworth specimen (two stems) is taken as the type.

Petalostemon griseum is very closely related to P. villosum: indeed, all the identifying characteristics of the former are found sporadically throughout the range of P. villosum. The possession of a specific array of characteristics in conjunction with allopatric distribution, however, is the basis for considering P. griseum a distinct species. Distinguishing between the two species in the field is relatively simple: P. griseum has fewer stems, grows taller, branches more profusely in the upper half and all spikes become long and nodding in fruit. Most of these characteristics cannot be readily transferred to herbarium sheets; thus, the correlation of several "minor" characteristics must be used for identification. In general, P. griseum 1) is less pubescent, 2) has reddish stems, 3) possesses larger leaflets, 4) often has "straggling" flowers below the main body of the spike, 5) has extremely long spikes, and, 6) has a broad, cordate standard. In conjunction with the earlier flower-

ing time and the geographic restriction to western Texas and eastern Louisiana, P. griseum can be recognized readily from herbarium specimens.

These species cannot be separated, either in the field or in the herbarium, on the basis of spreading of ascending leaves, calyx length or spike width as proposed by previous authors.

Description

Plants arising from a long, relatively unbranched, red taproot, which is up to 4 dm in length. Stems erect, reddish, finely striate, spreading ciliate but not villous; usually branched in the upper half, (4) 6-7 (9) dm tall, 4-5 mm thick at base. Stipules subulate, dark, 5-6 mm long. Leaves 2-4 cm long; rachis extended beyond the terminal pair of leaflets 1-2 mm; leaflets (9) 11-13 (15), oblong-elliptical, mucronate, slightly pubescent on both surfaces, but predominantly so on the lower surface, 10-15 mm long, 2.7-4.2 mm broad, not always perfectly paired on the rachis. Spike subsessile; the peduncle a maximum of 3 cm in length, often with straggling flowers near the apex; spike lax, flowering at 4 cm long and through further floral differentiation reaching a maximum length of 14 cm, becoming sinuous and nodding; (6) 7-9 mm in diameter. Bracts lanceolate, only slightly expanded proximally, exceeding the calyx in bud, usually falling before anthesis leaving a decided "heel" on the rachis. Calyx spreading-ciliate; the tube 10-ribbed, clearly visible, pale, slit dorsally to almost half its length. 2.0-2.2 mm long, 1.7-2.0 mm in diameter; ventral lobe 1.0-1.2 mm long, each lobe tipped with a minute gland. Corolla pale lavender; standard blade cordate, entire at apex, 2.1-2.6 mm long, 2.5-2.8 mm broad, arching over the other floral parts, the claw 2.3 mm long; apical petals oblong to slightly oblanceolate, 2.3-2.6 mm long, 1.0-1.2 mm wide, the claws 0.5 mm long; medial petals inserted lower than the lateral petals on the staminal tube. Staminal tube 3 mm long, equaling the length of the free filaments; anthers pale yellow. Ovary villous except at the extreme proximal end, 1.0-1.3 mm long, 0.8 mm in diameter; style 4 mm long, ciliate only on the proximal one-fourth. Pod not exserted beyond the calyx lobes, villous, thick walled.

Distribution and phenology

Limited to east Texas and western Louisiana. Restricted to sandy soils. Flowering from late May to late June, reaching a maximum approximately the second week of June.

16. PETALOSTEMON VILLOSUM Nutt. (Map 9; Figs. 10A; 12A)

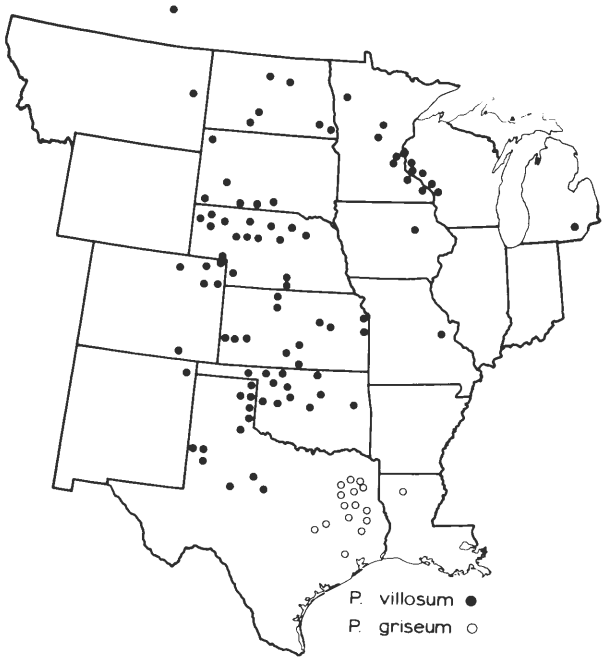
Petalostemon villosum Nutt. Gen. N. Am. Pl. 85. (1818). Type in PH. (1)(2).

Dalea villosa (Nutt.) Spreng. Syst. Veg. 3:326. (1826). Based on Petalostemon villosum Nutt.

Kuhnistera villosa (Nutt.) Kuntze. Rev. Gen. Pl. 1:192. (1891). Based on Petalostemon villosum Nutt.

Description

Taproot seldom branching, red, 2-4 dm long, usually equaling the stems in length. Stems many, radiating or ascending, often branching



Map 9. Geographic distribution of Petalostemon villosum and P. griseum.

near the apex, 2.5-3.5 (5) dm long, 3.5-5.0 mm thick at the base, densely villous, the pubescence often obscuring the stem surface. Stipules subulate, spreading-villous, 5-7 (9) mm long. Leaves fascicled, often crowded; rachis 1.5-3.0 (4.0 cm long, villous, bearing prominent, red "stipel-glands," 0.2 mm in diameter, below the petiole insertions; the midrib always extended 0.5-1.5 mm beyond the terminal pair of leaflets; leaflets 13-19 (21), gland-dotted below, long, appressed pubescence on both surfaces, 8.5-11.0 (13) mm long, 2-3 (3.5) mm broad. Spikes subsessile and lax, the rachis expanding following anthesis, often becoming sinuous in fruit, 4.5-11.0 (15) cm long, 8-10 (11) mm in diameter; sterile bracts often spread along the short peduncle below the spike. Bracts exceeding the calyx lobes in bud, villous throughout their length, 4-6 mm long, 1.2-1.4 mm broad, the acumen 2-4 mm long, usually deciduous immediately following anthesis. Calyx 10-ribbed, the surface often obscured by dense, spreading pubescence; the tube 2.0-2.4 mm long, split dorsally to one-third its length; the central lobe 0.9-1.4 mm long. Corolla lavender-purple to almost white; the standard blade never becoming erect and open but usually covering the other floral parts, 2.7 mm long, 2.0-2.5 mm broad, oblong to oval, sometimes truncate at the base, rarely cordate, often emarginate at the apex; the claw 2.3-2.5 mm long; apical petals obovate, 2.6-2.8 mm long, 1.0-1.2 mm wide, the claw short, 0.5 mm; medial petals inserted on the standard tube lower than the lateral pair. Staminal tube 2.2 mm long, the free filaments

3.7 mm long; anthers yellow to yellow-orange, exceeding the petal apices at anthesis. Ovary spreading-ciliate on the distal two-thirds, 1.0-1.1 mm long, 0.8 mm in diameter, the style 4.5 mm long, ciliate dorsally from the proximal end to barely one-third its length. Pod spreading-villous, exserted beyond the calyx lobes at maturity, the distal end bending upward between the dorsal calyx lobes.

Distribution and phenology

Restricted to sandy soils, sandhills and blowouts; ranging from southern Saskatchewan to northern Texas and from eastern Colorado to eastern Missouri. Flowering beginning in late June in the southern part of its range, mid-July in its northern part; most flowering terminated by mid-August.

Observations

This is a wide-ranging yet homogeneous species with a specific habitat preference for deep sand. Despite its ecological requirements in the field, it appears to grow and flower well in the greenhouse even though potted in Iowa prairie loam. Color variations are seen in the field as well as under greenhouse conditions, the petal colors ranging from almost white to light purple. The colors appear randomly distributed in most populations. Variations in degree of pubescence as well as leaflet number also exist but show no specific regional trends, indicative possibly of a genetic plasticity expressed as varying phenotypes. P. villosum is replaced in eastern Texas and western Louisiana by P. griseum, a species with which it shares many characteristics.

G. COMPACTI

Distinguishing characteristics

Root in most species a relatively unbranched taproot. Leaves solitary, seldom fascicled, the leaflets broad-elliptical to almost ovate. Spikes 1.0-2.0 cm in diameter with sterile bracts often found at the spike base. Fertile bracts concave, lanceolate to obovate with a strong midrib and scarious margins toward the proximal end, densely villous-sericeous, always exceeding the calyx lobes in bud and equaling or exceeding them in fruit. Calyx usually thin-walled and ciliate, the lobes villous-sericeous. Petals often inserted slightly below the apex of the androecial tube. Pod usually not exserted beyond the apex of the calyx lobes at maturity.

Distribution and ecology

Generally, plants of the west—south Texas through the Short Grass Plains to western Nebraska and Wyoming and west to the Continental Divide in the Columbia Plateau, southward to Nevada, Utah and northern Arizona. Most species are found in sandy soils.

Observations

This is perhaps an unnatural grouping, yet there appear to be pairs or trios of species that form links, one with another, which eventually tie all the species together. Petalostemon obovatum, a sand-dwelling endemic of south Texas, seems quite different from most species of Petalostemon, but has several characteristics in common with the rare Short Grass Prairie species, P. compactum. The latter species shares com-

mon characteristics with P. ornatum of the Columbia Plateau in the Pacific Northwest. P. flavescens of southeastern Utah seems related to both P. searlsiae of Nevada, Utah and Arizona and P. ornatum, thus completing the circle of species.

P. ornatum, P. compactum and P. flavescens all possess petals inserted slightly below the apex of the staminal tube. This characteristic is also shown by P. tenuifolium of the Purpurei group. This variation from true apical petal insertion, is very slight—observable only with 30X magnification or higher. The petals are much closer to the apex than in any species of Dalea I have examined.

Key to the Species

1. Calyx slit dorsally to half its length; calyx tube relatively thick, neither transparent nor long-ciliate, plants of the Great Basin.
   2. Corolla purple; calyx oblique, ventral calyx lobe 1.0-1.4 mm long; rachis elongating, spreading the calyces in fruit; spike over 4 cm long; plants of Nevada, adjacent counties in California, N.W. Arizona and W. Utah. 17. P. searlsiae
   2. Corolla yellow or yellowish-white; calyx not oblique, ventral calyx lobe 1.5-2.5 mm long, spike remaining compact in fruit, less than 4 cm long; plants of S.E. Utah and adjacent N. Arizona. 18. P. flavescens
1. Calyx not slit dorsally to half its length, calyx tube thin-walled, transparent, long-ciliate; plants of southern Texas, the High Plains or the Pacific Northwest.
   3. Corolla purple; stipules less than 3 mm long, plants of central Nevada and the Pacific Northwest. 19. P. ornatum
   3. Corolla yellow to yellowish-white; stipules longer than 3 mm, plants of the High Plains and southern Texas.
      4. Stems and leaves glabrous; leaflets elliptical-acute; peduncles 5-15 cm long; inflorescence less than 1.2 cm thick; plants of the High Plains. 20. P. compactum
      4. Stems and leaves pilose; leaflets broad-obovate; peduncles 1 cm long or shorter; inflorescence thicker than 1.2 cm. Plants of S. Texas. 21. P. obovatum

17. PETALOSTEMON SEARLSIAE Gray (Map 10)

Petalostemon searlsiae Gray. Proc. Am. Acad. 8:380. (1872). Type in GH. (1)(2).

Kuhnistera searlsiae (Gray) Kuntze. Rev. Gen. Pl. 1:192. (1891). Based on Petalostemon searlsiae Gray.

Description

Stems numerous, glabrous, often decumbent at the base, 3-5 dm long, glacous-green, conspicuously gland-dotted with red-brown protuberant glands, these more numerous and conspicuous toward the stem apex.

Stipules lance-subulate, deciduous, 1-2 (3) mm long. Leaves glabrous, usually solitary at nodes; rachis 1.5-2.5 (3.5) cm long with prominent "stipel-glands" below the petiolule insertions, extension beyond terminal pair of leaflets seldom over 1 mm; leaflets 5-7 (9), 9-16 mm long, 2-6 (8) mm broad, oblong to slightly obovate, often emarginate with a gland at the apex of the midrib, glandular below, smooth above; margins only slightly involute, but leaflets often folding when pressed, the midrib bending abaxially, especially so toward the leaflet apex. Peduncles long, 10-20 cm, glabrous, often with a few sterile bracts straggling below the main body of the spike. Inflorescence an expanding spike, compact in bud, becoming lax in fruit; spike 3-4 cm at anthesis, expanding to 6.5-9.0 (13) cm in length, 8-11 (12) mm wide; rachis glabrous to moderately pubescent, becoming visible in fruit. Bracts deciduous as spike expands, rhombic-lanceolate to oblanceolate, sometimes abruptly-acuminate, usually gradually narrowing to the acumen, which exceeds the calyx lobes in bud and equals or exceeds them at anthesis, usually abaxially reflexed in bud; distal portions usually ciliate, especially the margins, proximal portion usually glabrous, strongly clasping, slightly scarious laterally; total length of the bract 3.2-4.2 mm, breadth 0.8-1.2 mm. Calyx tube ± 10-ribbed, campanulate, oblique, slit dorsally to half its length, the margins of the slit ciliate; tube glabrous to puberulent, drying rufous, 2.4-2.8 mm long, 2.0-2.5 mm in diameter, usually possessing several yellowish glands lying between the calyx bundles; lobes drying black, spreading-ciliate, especially on margins, ventro-lateral lobes often directed slightly upward above the longitudinal calyx axis, leaving a gap between them and the ventral lobes, the ventral lobe 1.0-1.4 (2.0) mm long. Corolla rose-purple; standard blade rounded deltoid, sometimes slightly cordate, usually emarginate, 2.6-3.0 (3.2) mm wide, 2.7-3.1 (3.3) mm long; claw 3.0-4.0 mm long, emerging from the deep dorsal slit of the calyx; apical petals inserted at equal levels at the apex of androecial tube, blades oblong to slightly obovate, 3.3-4.2 mm long, 1.1-1.5 mm wide, claw 1.2-1.5 mm long. Androecial tube not exserted beyond the tip of the ventral calyx lobe at anthesis, 2.5-3.0 mm long; free filaments, 4.0-4.5 mm long. Carpel densely diliate on distal half, especially on upper surface, 1.5 mm long, 0.8-0.9 mm in diameter; style inserted on the longitudinal exis of the ovary or slightly below, ciliate proximally for more than half its length, 4.0-4.5 mm long. Pod villous at the distal end, protruding from calyx at maturity, the beak projecting between the dorsal calyx lobes.

Distribution and phenology

Restricted to Nevada, western Utah, southeastern California and northwestern Arizona. An abundant species found in dry gravelly or sandy soil usually associated with sagebrush and juniper. Flowering beginning in late April, reaching a peak at mid-May, ending by mid-June.

Observations

Bract shape appears to show a consistent regional variation. Most specimens from extreme southwestern Utah (Washington and Kane counties) have broader bracts, indicative of possible incipient regional patterning within the species. I have critically examined these specimens and find no further correlating characteristics that distinguish them from others throughout the range.

Petalostemon searlsiae is clearly distinct from P. ornatum even though the range of the two species is contiguous. P. searlsiae can always be distinguished by the possession of an elongating spike 12 mm or less in diameter and a calyx slit dorsally to half its length, the slit ciliate at the margins. The calyx is neither thin and papery nor sericeous-pilose as in P. ornatum; rather, it is thick, drying rufous, glabrous or short-puberulent. P. searlsiae differs in so many ways from P. ornatum that it is indeed unlikely that they are closely related; however, their common relationship to P. flavescens of southeastern Urah provides justification for their inclusion in a common group, Compacti.

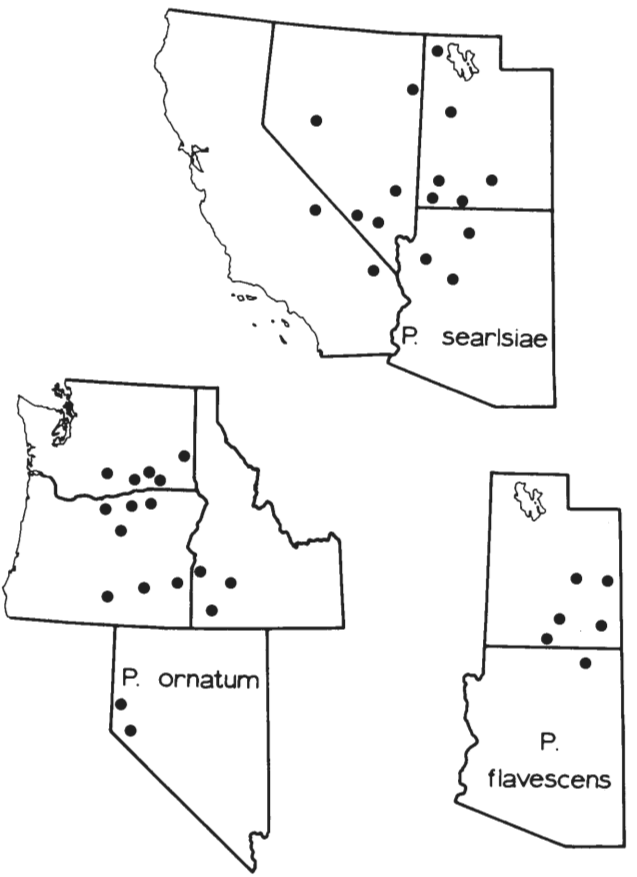
18. PETALOSTEMON FLAVESCENS Wats. (Map 10)

Petalostemon flavescens Wats. Amer. Nat. 7:299-200. (1873). Type in GH. (1)(2)

Kuhnistera flavescens (Wats.) Kuntze. Rev. Gen. Pl. 1:192. (1891). Based on Petalostemon flavescens Wats.

Description

Plants with stems 2-4 dm long, usually spreading-ciliate at base, becoming appressed-ciliate above, the entire stem covered with slightly protuberant glands. Stipules subulate, 2-4 mm long, ciliate. Leaves usually solitary, the rachis 1.5-2.5 cm long, often conspicuously gland-dotted, extended beyond the terminal pair of leaflets 1.0-1.7 mm; leaflets 5-7, elliptical to narrow-obovate, appressed-ciliate on both surfaces, rarely glabrous, 10-13 (16) mm long, 3-6 (7) mm wide, gland-dotted below, not above; often becoming conduplicately folded when dried, the midrib bending abaxially, the entire leaflet becoming falcate. Peduncle long, 7-15 (22) cm. Inflorescence a nonexpanding spike, 21-35 (55) mm long, 10 mm broad; rachis pubescent. Bracts narrow, lanceolate, only slightly expanded below the acumen, 5-8 mm long, 1.3-1.5 mm wide, exceeding the calyx lobes in bud, equaling or exceeding them at anthesis; proximal end "v-shaped" in cross section, the midrib prominent, usually ciliate, margins glabrous and slightly scarious; distal portion flat, not concave or "v-shaped," glandular, ciliate, narrowing to the acumen which is long-ciliate; small, paired, glandular bracteoles, 0.2 mm long, flank the base of the calyx. Calyx obviously 10-ribbed, the tube slightly thin-walled but not translucent, 2.6-3.0 mm long, streaked red, slit dorsally over half its length, the margin of the slit, ciliate, lobes lanceolate with ciliate, sometimes glandular margins, the ventral ones 1.5-2.5 mm long. Corolla yellow or yellow-white; standard oblong to rounded-deltoid, slightly cordate, emarginate at apex, 2.5-4.0 mm long, 1.5-3.8 mm broad, the claw 3.2 mm long; apical petals inserted at the same level, but slightly below apex of staminal tube, oblong, cuneate at the base, 2.6-5.0 mm long, 0.9-1.7 mm wide, the claw 1.2-1.6 mm long. Staminal tube 2.9-4.5 mm long; free filaments 3.0-6.0 mm long; anthers pale yellow. Ovary elliptical, 1.5-2.3 mm long, 0.8-1.2 mm in diameter, ciliate on distal half, mostly ventrally; style 6.0-8.0 mm long, ciliate dorsally from proximal end to half its length. Pod villous, not exserted beyond the calyx lobes at maturity.



Map 10. Geographic distribution of Petalostemon searlsiae, P. ornatum and P. flavescens.

Distribution and phenology

Rocky, sandy areas in southeastern Utah and northeastern Arizona. Apparently a very restricted and seldom collected species endemic to this area. Blooming time from late April to early June reaching a maximum in late May.

Observations

Petalostemon flavescens is highly variable for such a geographically restricted species. Vegetative pubescence varies from entirely glabrous to spreading-villous below and appressed-pubescent above. Floral parts also vary widely in size and shape. Standard shape fluctuates from oblong (quadrilateral, as described by Watson for the type) to rounded-deltoid. One specimen examined (Holmgren and Goddard 9990, San Juan Co., Utah) possesses a highly glandular calyx with large spherical, translucent glands on the margins of the lobes—strikingly different from others of the species.

Notwithstanding the individual variations, this species seems distinct and quite separate from others of this group. The closest affinities appear to be with P. searlsiae. The moderate pubescence, glandular bracts, relatively thick-walled, dorsally split calyx and the more oval ovary are characteristics in common. Similarity between the two species was noted by Jones (1895, p. 631) who wrote: "Petalostemon flavescens Watson seems to be a white flowered form of P. searlsiae. I can see no other valid difference." Jones' remarks are reflected by Rydberg (1919-1920) following his description of P. flavescens: "(Perhaps not distinct from P. searlsiae)." Despite this warning, Rydberg places P. flavescens in his "section" Compacti while placing P. searlsiae in Ornati.

P. flavescens is distinct from P. searlsiae on the basis of at least four characteristics. They are: 1) possession of a nonexpanding spike; 2) a yellow-white to white corolla contrasted with the purple corolla of P. searlsiae; and 3) longer calyx lobes. Petalostemon flavescens also shows certain characteristics in common with P. ornatum and P. compactum. The petals of P. flavescens are inserted slightly below the apex of the calyx lobes at maturity. It seems reasonable, therefore, to include all these species in a single group, Compacti.

19. PETALOSTEMON ORNATUM Dougl. in Hook. (Map 10)

Petalostemum ornatum Doug. in Hook. Fl. Bor. Am. 1:138. (1830). Type in GL. (1)(2).

Dalea ornatum (Dougl.) Eaton. Man. Bot. for N. Am. 120. (1833). Based on Petalostemon ornatum Dougl.

Petalostemon macrostachyum of T. and G. Fl. N. Am. 1:309. (1838). in part. Not Petalostemon macrostachyum Torr. (1828).

Kuhnistera ornata (Doug.) Kuntze. Rev. Gen. Pl. 1:192. (1891). Based on Petalostemon ornatum Dougl.

Petalostemon lagopus Rydb. Fl. N. Am. 24:134. (1919-1920). Type in NY. (1)(2).

Petalostemon ornatus f. pellidus St. John. Northwest Sci. 2:86. (1928). Type in WSP. (1)(2).

Nomenclature and observations

The specimen I accept as the type is in GL and is labeled in what I take to be Hooker's hand:

"Petalostemon macrostachyum Torrey
ornatum Douglas
North W. Coast
Hooker"

I am assured by the curator, Dr. I. M. Case, that no other material is available that might possibly be confused with this specimen. It does, however, lack any other markings that correlate with Douglas' collection data—"Frequent in the arid prairies near the Blue Mountains of Lewis River, North West America."

I have included within the delimitation of P. ornatum, Rydberg's taxon, P. lagopus. I have seen the type at NY as well as an isotype at US. Although collected far to the south (western Nevada, Truckee Pass, Washoe Co.) of the presumed distribution of P. ornatum, it is indistinguishable, morphologically, from the more northern collections. To my

knowledge this southern distribution is represented by only two collections. Rydberg (loc. cit.) separated the two species as follows:

"Bracts lanceolate, long attenuate, much exceeding the buds or calyces.

39. P. ornatum, Oregon and Washington

Bracts broadly obovate, abruptly acuminate, scarcely exceeding the buds or calyces.

40. P. lagopus, Idaho, Nevada and western Utah"

Among the plants examined from Washington and Oregon are found all shapes of bracts from narrow-lanceolate to rather broadly obovate, abruptly acuminate ones. Broad, short bracts, thus are not limited to the southern range. A further argument supporting merger of the two species is ecological. A finger of the "Sagebrush Steppe, Artemesia-Agropyron Association" extends south into western Nevada from the Columbia Plateau (Küchler 1964). Because of its southern occurrence, this material has been confused with P. searlsiae (Porter 1957). Specific differences between the two species are more fully discussed under P. searlsiae.

Description

Plants with reddish-colored roots giving rise to numerous, glabrous, green-glaucous stems, 3-5 dm long, often corky below, moderately striate on lower portions, strongly striate above, dotted with slightly protuberant brown-red glands that are most pronounced and numerous at the stem apex. Stipules short, lanceolate, 1.2-2.2 (3.0) mm long. Leaves solitary at nodes; rachis to 4.0 cm in length, margined and glandular with prominent "stipel-glands" immediately below each petiolule insertion; rachis always extended 1.5-3.0 mm beyond the terminal pair of leaflets. Leaflets 5-7, varying in shape from broad-elliptical or broadly obovate to orbicular, 11-25 mm long, 6-12 mm broad, often emarginate, pale green and smooth above, gray-green and ± prominently glandular below. Peduncles 2.5-10.0 cm long, usually at least one-fourth the total stem length; sterile bracts lacking below the inflorescence. Inflorescence a compact, nonexpanding spike 12-16 mm broad and to 57 mm long in fruit, usually conical in bud; rachis varying from glabrous to extremely pubescent. Bracts lanceolate, exceeding the calyx lobes in bud, equaling or exceeding them at anthesis, 0.8-1.8 mm wide, 4.0-5.6 mm long; proximal half clasping calyx, possessing a strong midrib and scarious lateral areas, usually glabrous but sometimes with a ciliate midrib; distal half flat, green, drying black, often with scattered glands, sericeous-long-ciliate, cilia to 1.5 mm long. Calyx tube campanulate, thin-walled often ± transparent with dark colored vascular bundles, 2.6-3.8 mm long, covered with long appressed trichomes, often with rows of glands visible between vascular bundles; calyx lobes deltoid, green—drying black, 1.2-2.0 mm long, sericeous, cilia to 1.8 mm long. Corolla pale lavender; the standard 2.4-3.0 mm wide, 2.7-4.0 mm long, the base often slightly cordate, the apex entire or moderately emarginate, claw 4.5-6.0 mm long; apical petals oblong to slightly oblanceolate, often inserted slightly below the apex of the androecial tube, the central pair inserted lower than the lateral pair, 3.5-4.7 mm long, 1.4-2.1 mm wide, the claws 1.2-1.7 mm long. Staminal tube about 4.5 mm long, the free

portion of the filaments 4.0-5.5 mm; anthers yellow. Carpel bearded, predominately so dorsally although ± pubescent over entire distal half; ovary 1.8-2.2 mm long, 1.0 mm in diameter; style inserted on the carpel axis, 8.0 mm long, ciliate dorsally from the proximal end to about half its length. Pod not exserted from calyx tube at maturity, pubescent distally, glabrous proximally, the style remnant directed upward between dorso-lateral lobes of calyx.

Distribution and phenology

Limited to the Columbia Plateau (Fenneman 1931) and adjacent areas to the south; within this geological area to the "Sagebrush Steppe, Artemesia-Agropyron Association" (Küchler 1964). Found on the bluffs, rocky hillsides and slopes in sands and sandy clays. Flowering period from early May to early July, peeking during the first week of June.

20. PETALOSTEMON COMPACTUM (Spreng.) Swezey (Map 11)

Petalostemon compactum (Spreng.) Swezey. Nebr. Fl. Pl. 1:6. (1891). Based on Dalea compacta Spreng.
Dalea compacta Spreng. Syst. Veg. 3:327. (1826). (2)(4).
Petalostemon macrostachyum Torr. Ann. Lyc. Nat. Hist. N.Y. 2:176-177. (1828). (2).
Kuhnistera compacta (Spreng.) Kuntze. Rev. Gen. Pl. 1:192. (1891). Based on Dalea compacta Spreng.

Nomenclature and observations

The nomenclatural problems involved in the adoption of P. compactum (Spreng.) Swezey are discussed by Isely (1962). In summary, the Sprengel description is inadequate and the Sprengel herbarium was broken up in the 1860's and a portion assumed to possess the sought-after material destroyed during World War II. P. macrostachyum, published 2 years subsequent to the Sprengel name is clearly identifiable but has not been used by Twentieth Century botanists because of its relation to synonymy by both Swezey and Kuntze. As to why Swezey and Kuntze placed the Torrey name in synonymy is not clear—neither offer an explanation. Isely concludes that it is probable that neither of the two could have had access to the Sprengel specimens or at least information about them on which to base their decisions.

Barneby proposes that the epithet P. compactum be ascribed to what I herein interpret as P. decumbens Nutt. primarily on the grounds that the specimen must have been collected by Nuttal along the Red River (Sprengel states, Ad Fl. Rio Roxo in ditione Arkansa Amer. bor.) and must therefore have been P. decumbens sensu Nutt. (pers. comm. to D. Isely, 22 October 1966).

The circumstantial evidence presented by Barneby deserves consideration. But lacking a type specimen I cannot presently justify his point of view; I leave subsequent documentation to him.

It is obvious that this taxon and P. ornatum are related. Both possess similar bract and calyx pubescence, thin, transparent calyces with red-black vascular bundles, petals inserted slightly below the apex of the androecial tube, elliptical, carpels and pods not exserted beyond the calyx lobes. The relationship of these two taxa was first suggested by Heller on an annotation label placed on a New Mexico collection of

P. compactum (Vasey 1881, Albuquerque). It reads: "Seems to be intermediate between K. ornata and K. compacta."

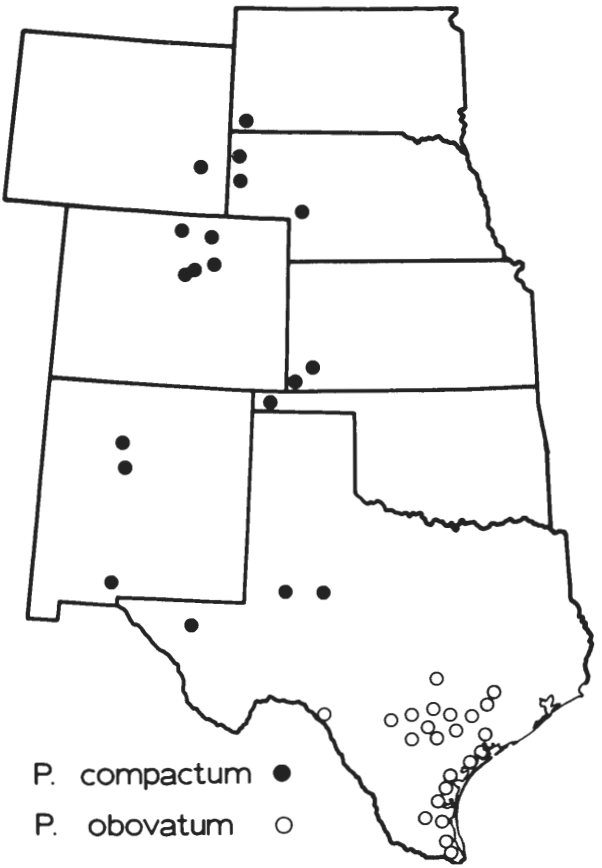
The corolla color of fresh material is said to be white to yellowish-white. When dried, the petals appear pale yellow. One collection from New Mexico (Ripley and Barneby 8347) seems to possess lavender petals. Close examination, however, shows it otherwise to fit clearly within the circumscription of P. compactum.

Description

Plants with relatively few stems branching from an orange-red taproot, 3-5 dm tall, erect, branching above, glabrous, pale straw-colored with prominent, slightly protuberant brown-red glands. Stipules 2.0-3.5 mm long; rachis extended 2-5 mm beyond terminal pair of leaflets; large "stipel glands" often present immediately below the petiolule insertions; leaflets 7-9 (11), elliptical, acute, to 25 mm long and 6 mm wide, usually four times as long as wide; pale green and nonglandular above, gray-green and glandular-punctate below, the glands generally restricted to areas near the margin of midrib. Peduncles 8-13 (15) cm long; glands protuberant, most numerous and pronounced near the apex. Inflorescence a nonexpanding, compact spike beginning anthesis when 2 cm long but through further floral differentiation, attaining length of 8-10 (12) cm with a breadth of 1.0-1.2 cm. Rachis 3 cm in diameter, densely spreading-villous, the cilia immediately below flowers retrorse; frequently with a whorl of sterile bracts at the base of the spike. Fertile bracts exceeding calyx lobes in bud and at anthesis, narrow-lanceolate with a prominent midrib proximally, 6-8 mm long, 0.5 mm wide, pubescence, spreading villous-sericeous, covering the surface distally, restricted to midrib proximally especially pronounced at margins, the trichomes 1.5 mm long; calyx tube thin-walled and relatively transparent, 1.8-2.2 mm long; vascular bundles drying red-black, visible through sericeous indument; lobes equaling tube, 1.6-2.2 (2.4) mm long, often not visible through the dense, spreading, cilia covering them. Corolla yellow-white (bluish in New Mexico ?); standard 1.8-2.2 mm long and as broad, rounded-deltoid, slightly cordate, the anterior margin often crenate; apical petals 2.0-3.2 mm long, 0.5-0.8 mm wide, oblong; claws 1.5 mm long, inserted just slightly below the apex of the standard tube, all at the same distance from the floral base. Androecial tube 3.0-3.2 mm long; free filaments 3.0-3.4 (4) mm long. Ovary elliptical 1.8-2.2 mm long, 0.7-0.9 mm in diameter, long ciliate on distal half; style 4.0-4.5 mm long, ciliate dorsally from the proximal end to one-third its length; stigma not exserted beyond anthers. Pod not exserted beyond the apices of the calyx lobes at maturity.

Distribution and phenology

Widely distributed but infrequent on the Great Plains from southwestern South Dakota to central New Mexico and west Texas. Apparently growing in a variety of habitats—sandhills, rocky slopes and knolls. Flowering time is sporadic, as early as late May and as late as late September. Maximum flowering is in mid to late July. The southern populations do not seem to flower earlier than those in the more northern part of the range.



Map 11. Geographic distribution of Petalostemon compactum and P. obovatum.

21. PETALOSTEMON OBOVATUM T. and G. (Map 11, Fig. 12E)

Petalostemon obovatum T. and G. Fl. N. Am. 1:310. (1838). Isotype in US. (1) (2).

Dalea agastachys Moric. Pl. Nouv. Am. 65-66, p. 44. (1839). Isotype in NY. (1) (2).

Kuhnistera agastachya (Moric.) Kuntze. Rev. Gen. Pl. 1:192. (1891). Based on Dalea agastachya Moric.

Kuhnistera obovata (T. and G.) Heller. Bull. Torr. Bot. Club. 23:122. (1896). Based on Petalostemon obovatum T. and G.

Nomenclature and observations

The publication of Moricand's Plantes nouvelles d'Amerique (loc. cit.) was spread over the years 1833-1846. There is no indication in the paper itself as to the dates of publication of the various parts. The exact date

of publication of pp. 65-66 is 1839, according to Rickett and Stafleu (1961), confirms the date cited by Heller (1896).

This species is unique in that it sets seeds freely even in the absence of insect pollinators. The free filaments are very short and do not diverge from the longitudinal floral axis as in all other species. At anthesis, the style is shorter than the anthers but gradually elongates, passing through the pollen masses held by the filaments and anthers thus effecting pollination. Another unique characteristic is the long, plumose calyx lobes, reminiscent of those found in subgenus Kuhnistera. P. obovatum seems most closely allied with P. compactum. Both share: 1) indeterminate spike growth with flowers developing apically while fruits are falling from the rachis below; 2) clustered sterile bracts at the base of the spike; and, 3) a densely villous-sericeous calyx with transparent tube and dark-colored vascular bundles.

Description

Plants arising from a long, relatively unbranched, yellow-red taproot. Stems 4-5 dm long and to 6 mm thick at the base, decumbent and unbranched below, erect and often branched above, spreading pilose throughout their length. Stipules 4-7 (10) mm long, lanceolate from a broad base, spreading pilose. Leaves 3-4 (4.5) cm long, often deciduous on lower portions of stems; rachis extended beyond distal pair of leaflets 2.5-4.5 mm; leaflets (7) 9-11 in number, 10-13 mm long, 5-8 mm wide, obovate, obtuse or emarginate at apex, appressed ciliate on both surfaces. Peduncles short or essentially nonexistent, a maximum of 1 cm long. Inflorescence a compact spike showing no rachis elongation in fruit, but increasing in length due to apical floral differentiation following anthesis of lower flowers (spike then about 4 cm long), reaching a maximum of 8-10 cm in fruit, 1.4-2.0 (2.4) cm in diameter; inflorescence subtended by a whorl of sterile bracts. Fertile bracts concave, obovate, about 8.0 mm long, 3.3 mm wide, conspicuously glandular on the abaxial surface, pilose, spreading-ciliate, the trichomes 2.0 mm long; bract body 4.5 mm long, gradually tapering to an acumen 3.5 mm long, the tip drying dark red-brown; entire bract exceeding calyx lobes both in bud and in fruit; proximal portion of bract strongly "v-shaped"; margins scarious. Calyx tube transparent, spreading-villous, 2.2-2.5 mm long, the vascular bundles drying red, clearly visible through the dense pubescence; lobes plumose, equaling or exceeding tube, subulate from a broad base, 2.0-3.0 mm long, the sinuses rounded between lobes. Corolla yellowish-white; standard 3.0-3.3 mm long, 1.6-1.8 mm wide, somewhat rectangular, truncate or slightly emarginate at apex, surpassing other floral parts following anthesis; claw 3.8-4.7 mm long; apical petals 2.8-3.4 mm long, 1.0 mm wide, rounded-oblong to obovate, the claws 0.6 mm long, inserted at the apex of the staminal tube. Androecial tube 4.6-5.0 mm long, the filaments 2.5-3.0 mm long, not spreading from longitudinal floral axis, the pale yellow anthers equaling the stigma in exsertion. Ovary 1.6-1.7 mm long, 1.0-1.1 mm in diameter, densely villous in its entirety, the cilia especially prominent distally; style 5 mm long, ciliate only at the very proximal end. Pod spreading-villous, not surpassing calyx lobes at maturity.

Distribution and phenology

Restricted to the "deep sands" (Gould 1962) of south Texas, usually growing in association with Dalea emarginata. Flowering from early April to mid-July.

H. PURPUREI

Distinguishing characteristics

Leaves with (3) 5-9 (13) leaflets. Bracts and calyces with ± appressed, usually short pubescence; calyces lacking prominent ribbing; corollas purple; anthers orange-yellow.

Distribution and ecology

Restricted to the Great Plains and Prairies. None extend west of the Continental Divide and few penetrate into the Gulf Coastal Plain. Most appear to be calciphilic, growing either on limestone substrates or calcareous prairie soils.

Observations

Even though some species characteristically have leaves with a maximum number of leaflets greater than 5, pentafoliate leaves predominate in this group. Trifoliate leaves are generally found only near the stem tips or stem bases (first formed leaves). Bract and calyx pubescence is short, often appressed, but sometimes spreading. Most species possess bracts that are glabrous except for a transverse belt of appressed cilia immediately below the base of the acumen, but in others, the bracts are uniformly pubescent. Calyx pubescence is uniform in some species but varying degrees of "balding" also occur. The extreme condition is reached in P. pulcherrimum, in which only an appressed fringe of hairs is found on the lateral margins of the calyx tube. In all species, the calyx is seldom prominently 10-ribbed, the vascular bundles supplying the lobes seem deeply imbedded within the tissues of the calyx wall and show little sclerification. P. tenuifolium shows moderate ribbing, but it is generally concealed by the typical spreading pubescence of this species. All taxa possess a purplish corolla with a range between species from pale lavender through blue to red-purple. There is little variation within single species and most populations appear quite uniform in this characteristic. Compatibility tests carried on over the past 3 years have shown that all species of the complex are interfertile; furthermore, the progeny show no abnormal meiotic divisions or reduction in viable pollen.

There can be discerned three morphological units within the complex which are marked by variations in calyx shape. One group, perhaps the most generalized, is represented by P. purpureum, the most wide-ranging species of the complex. This species possesses a tubular calyx of intermediate length (2.5-4.0 mm). The bract bodies are invested with a transverse belt of cilia, the remainder of the bract is glabrous.

P. gattingeri, P. tenue, P. arenicola, P. tenuifolium and P. reverchonii form another group, all possessing short (2.0-3.0 mm) campanulate calyces and narrow spikes. Generally the lobes are longer in relation to the calyx tube than in the other two groups. Even though uniform in major characteristics, there is considerable diversity within this group. For example, P. gattingeri, P. reverchonii and P. tenuifolium

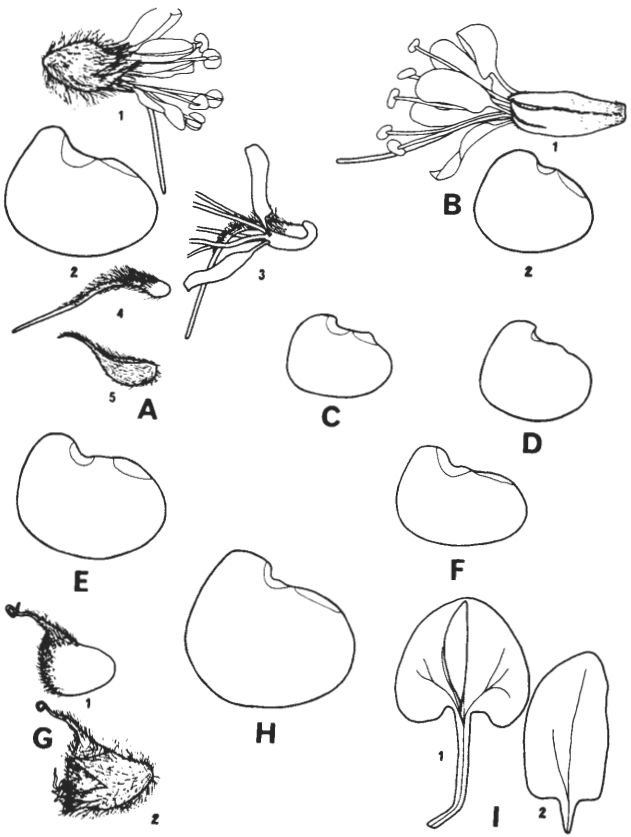


Figure 11. Floral parts and seeds of species in section Purpurei. All floral drawings except I are x5. All seeds and the petals in I are x15.

A. P. tenuifolium. 1. lateral view of flower. 2. seed. 3. androecium and gynoecium, standard removed. 4. carpel. 5. bract.

B. P. decumbens. 1. lateral view of flowers. 2. seed.

C. P. purpureum, seed. D. P. tenue, seed.
E. P. reverchonii, seed. F. P. gattingeri, seed.
G. P. tenuifolium x P. gattingeri. 1. legume. 2. fruit.
H. P. pulcherrimum, seed. I. P. arenicolia. 1. standard (folded in the center due to concave shape). 2. apical petal.

all possess a rachis that elongates following anthesis, but both P. tenue and P. arenicola retain a compact spike even in fruit. There is also variation in calyx pubescence, from the spreading investure of P. tennuifolium to the retrorse cilia of P. tenue. Although leaflet number is quite homogeneous in this group, the unusual, high leaflet number of P. reverchonii sets it quite apart from its associates. P. tenuifolium seems to represent the closest line to the P. purpureum tubular calyx form in closely resembling some of the "molle-pubescens" specimens of the western range of P. purpureum. The latter show a slight tendency for rachis elongation and short, almost campanulate calyx tubes, but retain all the other P. purpureum characters. On the other hand, P. tenue, even though specialized in the possession of retrorse pubescence, seems related in certain characteristics to the last unit of the complex, which is represented by P. decumbens and P. pulcherrimum. These two species have long, tubular, parchment-like calyces that are basally-rounded deltoid in cross section and possess short, incurved lobes. The dorso-lateral lobes arise from flat surfaces and the three ventral lobes from the hemispherical lower part of the tube. The calyx of P. tenue is similarly shaped. Calyx pubescence is limited in both species: in P. pulcherrimum, it consists of a fringe along the lateral angles, in P. decumbens, of a distal-lateral fringe plus generalized pubescence toward the base of the calyx. Both species have glabrous ovaries or nearly so, a condition also found in P. tenue.

Hybridization in field populations of Petalostemon is apparently rare. I have observed it only in P. decumbens, P. pulcherrimum, and P. purpureum, and then only in the contiguous southeastern Oklahoma counties: Marshall, Bryan, Choctaw and McCurtain. Detailed analyses of these hybrid populations will be treated in a subsequent publication. Hybridization between P. purpureum and P. gattingeri has been observed in central Tennessee by Miss Sally Walker of Vanderbilt University (pers. comm. 1966).

Key to the Species

1. Rachis elongating following anthesis, the raceme becoming lax; bracts fugacious, evenly pubescent, the cilia not restricted to a narrow, transverse, appressed band at the base of the acumen; calyx evenly pubescent with short, spreading indument.

   2. Leaflets 9-11 (13); stems less than 2 dm tall; rare, known only from type locality, Hood Co., Texas. 22. P. reverchonii

   2. Leaflets 3-19; stems longer than 2 dm; not restricted as above.

      3. Leaflets 3-5; stem base and apex of long peduncle with dense spreading pubescence; bracts 2 mm broad or more; north Texas and adjacent areas. 23. P. tenuifolium

      3. Leaflets 7-9; stem glabrous at base becoming slightly ciliate above, usually densely ciliate at apex of the short pedundle; bracts less than 2 mm broad; central Tennessee, northwest Georgia and Alabama. 24. P. gattingeri

1. Rachis not elongating following anthesis, the raceme remaining compact; bracts persistent, not evenly pubescent, the pubescence restricted to a narrow, transverse, appressed band at the base of the acumen; calyx often unevenly pubescent, the cilia ± appressed.

   4. Pubescence on distal 2/3 of calyx tube restricted to two bands of appressed cilia on lateral angles; spikes at anthesis usually 12 mm or more in diameter; leaflet number 7-9; restricted to southeastern Oklahoma and Texas.

      5. Bracts shorter than calyx lobes at anthesis; leaflets less than 3 mm wide; peduncles 4 cm or longer; east-central Texas and adjacent counties in southern Oklahoma. 25. P. pulcherrimum

      5. Bracts equaling or exceeding calyx lobes at anthesis; leaflets wider than 3 mm; peduncles 3 cm or less, spikes often subsessile; restricted to southeastern Oklahoma and southeastern Texas. 26. P. decumbens

   4. Pubescence on distal 2/3 of calyx tube not restricted to lateral bands; spikes at anthesis usually less than 12 mm in diameter; leaflet number usually 5, rarely 7; not geographically restricted as above.

      6. Plants ± pubescent with stems longer than 3.5 dm, usually branching above; peduncles short, less than 1/4 the length of the stems; spikes at anthesis 10 mm in diameter or wider; widespread from Canada to north Texas and Illinois to Colorado. 27. P. purpureum

      6. Plants usually completely glabrous with stems shorter than 3.5 dm, usually unbranched above; peduncles long, usually exceeding 1/4 the length of the stems; spikes at anthesis narrower than 10 mm; restricted to Texas and the Llano Estacado.

         7. Proximal calyx pubescence retrorse, directed toward the rachis; ovary glabrous or nearly so; central and east-central Texas. 28. P. tenue

         7. Proximal calyx pubescence antrorse, directed away from the rachis; ovary bearded; Llano Estacado. 29. P. arenicola

22. PETALOSTEMON REVERCHONII Wats. (Map 12, Fig. 11E)

Petalostemon reverchoni Wats. Proc. Amer. Acad. 21:449. (1886). Type in GH. (1) (2).
Kuhnistera reverchoni (Wats.) Heller. Bull. Torr. Bot. Club 23:124. (1896). Based on Petalostemon reverchoni Wats.
Dalea reverchoni (Wats.) Shinners. Field and Lab. 17:84. (1949). Based on Petalostemon reverchoni Wats.

Nomenclature and observations

According to the description, the type collection was, ". . .On the

rocky top ot Comanche Peak, in western Texas; J. Reverchon. June 1882 (n. 36)." I have seen two collections labeled No. 36. I accept as the type the specimen in GH; the other, an isotype, is at SMU. There are three additional Reverchon sheets also labeled Comanche Peak, June 1882 but numbered 1273, in NY, MO, and US. It is possible that there was a discrepancy in Reverchon's numbering system. For the present these sheets are assumed to be topotypes. The last collection of this taxon was in 1900 by H. Eggert (MO). This specimen, collected 5 June 1900 is in bud, clearly showing the precocious development of the bracts. The Reverchon specimens are, for the main part, fully in fruit but do possess small, secondary, axillary spikes at anthesis. There are few flowers on the latter spikes but the corolla color is retained. The corolla dimensions used in the description were extrapolated from a floral drawing on a Reverchon, 36 sheet at NY. The drawing of the calyx on that sheet is quite accurate and I have assumed the same true of the corolla. I have compared this artist's drawings on other sheets with my own observations and found them consistently accurate.

P. reverchonii represents somewhat of an enigma. It fits clearly within this section of the genus on all characteristics except leaflet number and the possession of pubescent stems while having relatively glabrous foliage. It has the elongating rachis characteristic of P. tenuifolium, yet the restricted bract pubescence and ciliation of P. arenicola. It is clearly related to the last two species as well as P. tenue on the basis of calyx shape. Its location is within the current geographic range of P. tenue and apparently occupies the same "ecological niche." Evidence for this is given by Shinners (1949b), who says:

> This is one of the most highly restricted endemics in north Texas. Comanche Peak is a massive, flat-topped outlier capped by one of the resistant limestone formations which make up the Edwards Plateau farther south and west. On the Edwards Plateau, the Comanche Peak limestone lies beneath other beds, but is exposed at many places in the intervening 'Lampasas Cut Plain' and elsewhere. Quite possibly the actual range of Dalea reverchonii is greater than known at the present.

Turner (1959, pp. 165-166) comments, "It is close to P. purpureum and P. pulcherrimum but seems to have a combination of characters that mark it distinct. However, detailed study of the entire P. purpureum complex may necessitate a change in its status." My study does not indicate that any change is in order regarding the status of P. reverchonii—it is distinctive but appears to belong clearly in the P. purpureum complex.

It is quite possible that P. reverchonii is no longer extant. For unlike P. sabinale, also a very rarely collected Texas endemic, P. reverchonii is not indivenous to a relatively remote, inaccessible area. Considering the close proximity to major botanical institutions, it seems unlikely that this species would not be collected if it was still in existence.

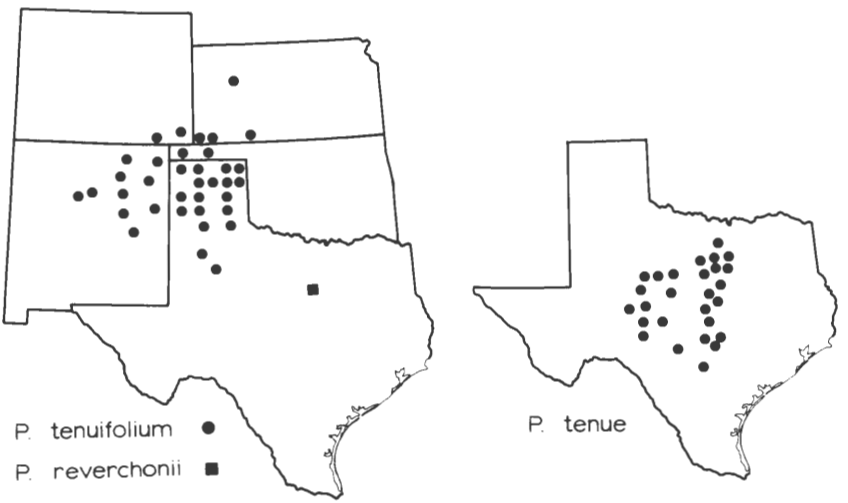
Description

Stems multiple, arising from a stout rootstock, 1-2 dm long, ± densely appressed-pubescent, striate, with three prominent ribs below each leaf. Stipules persistent, subulate, to 3 mm long. Leaves glabrous to glabrate,

fascicled, bearing 9-11 (13) linear-elliptical, incolute leaflets 5-8 mm long, 1.5 mm wide, glabrous, pale, and nonglandular below. Peduncles short, less than 10 mm in length. Inflorescence an expanding spike originating as a subglobose bud, attaining 7 cm in fruit, 1 cm thick. Bracts fugacious as rachis elongates, precocious, shorter than calyx lobes at anthesis, pubescent over the entire distal portion, the cilia not restricted to a narrow band, ciliate-fringed on the proximal margins. Calyx tube campanulate, evenly short-spreading—to slightly appressed-pubescent, 2.2 mm long, 2.4 mm in diameter; ventral lobe 1.8 mm long. Corolla deep pink or reddish, standard not lobed at base nor emarginate at apex, 2 mm wide, 2 mm long; apical petals oblong, 2.5 mm long, 0.9 mm wide. Ovary slightly pubescent distally and ventrally, style inserted above the longitudinal axis. Pods developing ventrally and distally, pushing up between dorso-lateral lobes in fruit.

Distribution and phenology

Known only from the type locality, Comanche Peak, Hood Co., Texas. The two (three?) collections were made in June, the one labeled 5 June 1900 by H. Eggert, is in bud. the other, simply labeled June by J. Reverchon, 1882, has some spikes initiating anthesis and some in full fruit.



Map 12. Geographic distribution of Petalostemon tenue, P. tenuifolium and P. reverchonii.

23. PETALOSTEMON TENUIFOLIUM Gray (Map 12, Fig. 11A)

Petalostemon tenuifolius Gray. Proc. Amer. Acad. 11:73-74. (1876). Type in GH. (1) (2).

Kuhnistera tenuifolia (Gray) Kuntze. Rev. Gen. Pl. 1:192. (1891). Based on Petalostemon tenuifolius Gray.

Petalostemon porterianus Small. Fl. S.E.U.S. 631. (1903). Original material in GH. (1) (2).

Petalostemon rothrockii Rydb. Fl. N. Am. 24:134-135. (1919-1920). Type in NY. (1) (2).

Dalea tenuifolia (Gray) Shinners. Field and Lab. 17:84. (1949). Based on Petalostemon tenuifolius Gray.

Nomenclature

A single type sheet bearing specimens representing many of the names that have been applied to this taxon is in GH. The primary label at the lower right hand corner reads, "Petalostemon tenuifolius n. sp., Dr. J. T. Rothrock, No. 81, Explorations and Surveys West of the 100th Meridian, Corps of Engineers, U. S. Army, Expedition of 1874." Four specimens on the right side of the sheet (an entire branch, and three separate stems) are mounted over the penned inscription, "Crossing of Red River, Arkansas, Dr. Newberry." At the upper left-hand corner of the sheet is a handwritten note signed by T. C. Porter reading:

> Petalostemon [in ink] Searlsiae ? [in pencil] Dalea ? Allied to D. filiformis, Gr. (Pl. Wright. 1. 0. 39) but differs: Fruticulose at base—pubescent—leaves glandular—bracts broadly ovate and cuspidate—flowering spike larger and fruiting ones larger, 1'-3'. On route from Leavenworth to El Paso. Legit F. R. Diefendorfer.

All this coincides with Gray's complex type citation in the description as, ". . . Arkansas, at the crossing of Red River, Dr. Newberry; New Mexico, Mr. Dieffendorfer (ex T. C. Porter), J. T. Rothrock."

That this sheet also contains material referable to a type of P. porterianus Small is less clear. Small names no type nor does he cite specimens. He merely states, "On prairies, Arkansas, Summer." Further, there is evidently no material in NY annotated by Small as P. porterianus. The principal clue then is that the name suggests a Porter collection or at least one on which Porter supplied the information. Seemingly of this mind, Rydberg (1919-1920) states at the close of his description, "Type locality: 'Leavenworth, Arkansas, to El Paso, Texas'." I take this to mean a designation by Rydberg of this specimen. In corroboration is a pencilled arrow pointing to a stem below Porter's note on the subject sheet, followed by, "P. porterianus Small," signed "PAR" in Rydberg's hand. Inasmuch as Rydberg's interpretation is plausible and the specimen is consistent with Small's description, acceptance of this specimen as the type seems reasonable.

The primary difference among the specimens on this intricate sheet is that the calyx ribs are slightly more prominent on that presumed to represent P. porterianus than that of P. tenuifolium. This, in fact, was the main criterion on which the separation of the two was originally based. My experience has indicated that throughout the range of P. tenuifolium the calyx is ribbed, but spreading pubescence often obscures this. The specimen on the left of this sheet (that representing P. porterianus) is more mature; the spikes have lost their bracts and the calyces some of their pubescence: Therefore, the calyx ribbing is easily visible. The other differences stated by Small and amplified by Rydberg are well within the range of P. tenuifolium as I understand it.

The species P. rothrockii is based on a specimen supposedly collected in Arizona. Barneby (pers. comm. 1966) believes it a duplicate of Rothrock 81, the typus of P. tenuifolium and actually collected in San Doval

County, New Mexico. Barneby says, "Many of Rothrock's collections at New York are poorly or quite incorrectly labeled, and this is surely one of them."

Description

Stems moderately striate, 2-5 dm tell, often branching above, slightly pubescent overall, with dense spreading cilia (to 0.5 mm long) prominent at the stem base and again just below the inflorescence. Stipules subulate, dark, to 5 mm long. Leaves fascicled; leaflets linear, 3-5, slightly ciliate at margins, involute, often curving when dried. Peduncles variable in length, 0.9-12.5 cm, elongating in age. Bracts precocious, exceeding the calyx lobes in bud, usually deciduous by anthesis, concomitant with rachis elongation; not clasping calyx at base nor strongly keeled, 2 mm broad or greater at expanded portion, 2.5-3.0 mm long, narrowing gradually to the dark, subulate acumen, 0.7-0.9 mm long; entire surface evenly pubescent; anterior edge rounded, ciliate-fringed. Inflorescence globose in bud, becoming columnar; rachis elongating following anthesis, the raceme becoming lax and often sinuous, up to 10 cm long, 7-10 mm wide. Calyx 10-ribbed, often barely visible through spreading pubescence of hairs up to 1 mm long; tube campanulate, 2.4-2.8 mm long; dorso-lateral lobes deltoid, ventro-lateral and ventral lobes lanceolate, the latter 1.7-2.0 mm long. Corolla violet to purple; standard blade 2.0-2.2 mm long, 2.0-2.3 mm wide, strongly auricled, the claw 2.2-3.3 mm long; apical petals inserted slightly below the apex of the staminal tube in prominent sockets, the blades 3.0-3.5 mm long, 1.0-1.5 mm wide, squared at the base but not auricled, claws 0.7-1.3 mm long. Anthers extended slightly farther than petal apices; pollen a bright yellow. Ovary 1.9-2.2 mm long, 0.8-1.1 mm in diameter, densely bearded on the distal half, the beard most prominently developed ventrally; pubescence continuing distally on the dorsal surface of the style for slightly over half its length; style inserted above the longitudinal axis of the carpel and in fruit directed upward at a 45° angle due to ventral development of the pod.

Distribution and phenology

Southwestern Kansas, southeastern Colorado, northeastern New Mexico and the panhandles of Oklahoma and Texas. Growing in rocky limestone soils usually in unprotected areas. Initiating anthesis in early May but not reaching maximum until early June, then tapering off until late July. A few collections have been made even later in the season, perhaps flowering at this time due to late season rains.

Observations

The range of P. tenuifolium is the southern part of the Llano Estacado and west into northern New Mexico. In parts of its range it is sympatric with P. purpureum and P. arenicola. It can readily be distinguished from both by its unique rachis elongation and spreading pubescence at the stem base.

The habitat preference of P. tenuifolium is on the mesa tops, the limestone cap rocks of the Llano Estacado. This contrasts with the habitat preference of P. arenicola, the sandy stream beds dissecting this area, and that of P. purpureum, the relatively rich but rare prairie soils of this general area.

P. tenuifolium is the only species of section Purpurei showing petal insertion slightly below the apex of the staminal tube. This characteristic is considerably more common in section Ornati. In all other characteristics, however, P. tenuifolium clearly fits into the Purpurei. The occurrence of this presumed "daleoid" characteristic in two sections of Petalostemon (and among species clearly Petalostemon on the basis of other characters) strongly suggests that this type of petal insertion is a secondarily derived feature. There is no indication of affinity with those Daleae with subterminal petal articulation.

24. PETALOSTEMON GATTINGERI (Heller) Heller (Map 13, Fig. 11F)

Petalostemon gattingeri (Heller) Heller. Bull. Torr. Bot. Club 26: 593. (1899). Based on Kuhnistera gattingeri Heller.
Kuhnistera gattingeri Heller. Bull. Torr. Bot. Club 23:121 and pl. 262. (1896). Type in US. (1) (2).

Nomenclature and observations

Although Heller, in naming the species in honor of Dr. A. Gattinger, did not single out a specific sheet, he did comment that, "Some of his [Gattinger's] specimens are in Curtiss' North American Plants, no. 565." I have seen five sheets so designated, (SMU, TENN, GA, 2—US). By far the best specimen is at US, and I designate it as the lectotype, US 24537.

P. gattingeri is an element of a flora endemic to the Cedar Glades of Central Tennessee and adjacent areas. The glades are a part of the Central or Nashville Basin (Quarterman 1950) and occur where the usual rolling upland pastures and alluvial farm lands are eroded away exposing horizontal layers of Lebanon limestone and Ordovician sediment. These strata are impervious to water and at certain times of the year are submerged. Some drainage is accomplished through small sink holes and vertical fissures which fill with soil allowing growth of clumps or rows of trees or larger shrubs. The strata themselves are often covered with a thin layer of soil varying up to one foot in depth. It is in this substrate that P. gattingeri grows. Quarterman classified P. gattingeri as a "characteristic species"; i.e., it was found in over 80% of the glade areas she examined. Nostoc commune Vauch, and Aristida longispica Poir. were the only other two species so recognized, but the glades contain numerous other endemics. Quarterman presents two hypotheses to explain the characteristic flora of the glades; 1) "The occurrence of both wet and dry extremes must limit the number of species capable of living in glade areas" and 2) "Restriction of certain species to glades is probably also affected by their inability to compete with mesic species in more favorable habitats."

Dolomitic limestone glades also occur in east central Missouri and many of the same species are found in these glades, but Petalostemon gattingeri is not among them. I have collected P. purpureum from one such glade in the Missouri Botanical Garden arboretum, Franklin County, Missouri (Wemple 478). This plant appeared no different from the typical prairie form of P. purpureum elsewhere in Missouri.

Under greenhouse cultivation, the matted growth habit of P. gattingeri remains constant as do all the other distinctive floral characters. Progeny grown from field collected seeds were uniform, growing and flowering with no special care beyond that given to other species of Petalostemon.

Description

Root black, massive and highly ramified, usually branching laterally immediately below the caudex. Stems many, branched, 2-4 dm long; glabrous and round at the base, becoming slightly ciliate and striate above, usually prostrate, inner ones erect, plants forming low growing mats. Stipules subulate, 5-7 mm long, persistent and drying straw colored. Leaves fascicled, the major leaf often with two minor trifoliate axillary leaves, occasionally an entire compressed branch system; mature leaf rachis to 20 mm in length bearing 7-9 narrow-lanceolate leaflets 10-14 mm long, 0.9-2.3 mm wide, usually near 1 mm, the wider leaflets restricted to leaves at the base of stems; leaflets moderately involute, drying pale green above, darker below with small, red glands visible only on the lower surface. Peduncles short, less than 3 cm, often lacking; apex becoming densely ciliate. Inflorescence an expanded columnar spike often becoming sinuous in fruit, 70 mm in length, never exceeding 10 mm in width, bracts precocious, far exceeding the calyx lobes in bud and equaling or slightly exceeding them at anthesis, fugacious as spike expands; body 1.5 mm long, elliptical, not tightly compressing calyx at base; bract pubescence evenly spreading over distal surface, not restricted to a narrow belt; distal-lateral margin fringed, the proximal end glabrous; acumen subulate, to 6 mm, often ciliate and recurved abaxially, especially in bud. Calyx tube campanulate, 10-ribbed, 2.0-2.6 mm long, evenly, densely pubescent; trichomes 0.7 mm long, drying silvery over the pale rust colored tube; lobes evenly ciliate, lanceolate, often spreading away from longitudinal calyx axis, the ventral lobe 1.7-2.5 mm, green in color persistent through drying. Corolla pale to deep purple; standard blade 2.3-2.6 mm wide, 1.4-2.0 mm long, deltoid, not auricled at base, the distal margin entire; claw 3.0-4.0 mm long; the apical petal lamina oblong-elliptical, 3.0-3.4 mm long, 1.3-1.4 mm wide, the claws 1.2-1.3 mm, cuneate at lamina base. Androecial tube 3.2 mm long, not exserted beyond calyx lobes; filaments 5.0-5.5 mm, purple, exserted beyond petal apices; anthers yellow-orange with lateral dehiscence lines bright red; pollen a bright orange. Ovary 1.2 mm long, 1.0 mm in diameter, strongly bearded on the distal-ventral 2/3, the style 8.0 mm, bearded dorsally and proximally, 1/3 to 1/2 its length.

Distribution and phenology

Central Basin of Tennessee, northwestern Georgia and northwestern Alabama. Restricted to glade environments. Initiatint anthesis in early May, reaching a peak at the middle of that month and gradually decreasing. Flowering may, however, continue to early August, due to secondary, axillary blooming.

25. PETALOSTEMON PULCHERRIMUM (Heller) Heller (Map 14, Fig. 11H)

Petalostemon pulcherrimum (Heller) (Heller, Bull. Torr. Bot. Club 26:593. (1899). Based on Kuhnistera pulcherrima Heller.

Petalostemon virgatum Scheele. Linnaea 21:461. (1848). (2). Not P. virgatum Nees von Esenbeck. (1840).

Petalostemon violaceum var. pubescens Gray. Smith. Contr. Knowledge 3:46. (1852). Based on Petalostemon virgatum Scheele.

Kuhnistera pulcherrima Heller. Contrib. Herb. Franklin and Marshall College 1:50-51. (1895). Based on Petalostemon virgatum Scheele.

Petalostemon pubescens (Gray) Heller. Muhlenbergia 1:28. (1901). Based on Petalostemon violaceum var. pubescens Gray. Not Petalostemon pubescens A. Nels. (1901).

Dalea stanfieldii (Small) Shinners (in part). Field and Lab. 17:84. (1949). Based on Petalostemon stanfieldii Small.

Dalea helleri Shinners. Field and Lab. 21:165. (1953). Based on Petalostemon virgatum Scheele.

Nomenclature and observations

Adolf Scheele (loc. cit.) was the first to apply a name to this species. His description is lucid and concise, clearly setting it apart from P. violaceum (P. purpureum). Unfortunately, his name, P. virgatum, had been preempted 9 years earlier by Nees von Esenbeck and is now in synonymy under P. occidentale. It is probable that Asa Gray, the next person to deal with the nomenclature of this taxon, did not realize that Scheele's name was a later homonym. Gray's work has been discussed in detail by Heller (1901). The following is but a brief review:

> Gray in Plantae Lindheimerianae (1850) stated in a footnote (p. 176): 'Petalostemon virgatum, Scheele, in Linnaea, 21, p. 461, is plainly the No. 42, Pl. Lind. [of Lindheimer] and No. 137, Pl. Fendl. [of Fendler], viz. a pubescent variety of P. violaceum, perhaps connecting that species with P. decumbens.'

I have examined the three sheets making up Lindheimer 42 (GH), and they are clearly P. pulcherrimum (Scheele's P. virgatum). The single sheet, Fendler 137, is definitely not the same species, but rather it is what Gray accurately described— "a pubescent variety of P. violaceum" (P. purpureum). In short, Gray misinterpreted Scheele's concept of P. virgatum, or perhaps as Heller (loc. cit.) put it, ". . . Dr. Gray very much underrated the excellent work of Scheele, refusing, at least for a time, to recognize some very good species which he described.

Gray (loc. cit.) published P. violaceum var. pubescens but further compounded nomenclatural problems by writing (p. 46):

> 137. Petalostemon violaceum, Michx., var. pubescens (Gray, Pl. Fendl. p. 33). P. virgatum, Scheele in Linnaea, 21. p 461. Prairies, Austin, Texas. —From the Snake Country, in the interior of Oregon, Mr. Burke sent to Sir Wm. Hooker dwarf specimens of this variety, and from the Black Hills of the Platte both Burke and Gordon have sent others, with densely pubescent leaves and even tomentose stems, which I cannot otherwise distinguish from this species.

This discussion presents two nomenclatural problems. First, Gray's citation back to his preceding publication, Plantae Fendlerianae (1849), is incorrect because there, under No. 137, Gray had: "P. violaceum Michx. . . . a pubescent variety; the calyx very silky-villous. Five miles west of Las Vegas, New Mexico; August." This is not a valid publication of a new variety. Secondly, his use of the Scheele name as a synonym follows that in his Plantae Lindheimerianae (1850) discussion,

but he cites the Burke and Gordon specimens as representatives of this new taxon. I have examined one of Burke's sheets (NY, unnumbered, Snake River Country), and it fits into the general range of variation of P. purpureum. Even though Gray obviously intended this name for the extremely pubescent forms of P. purpureum, still, according to nomenclatural practice, the name P. violaceum var. pubescens is legally based on the description of P. virgatum Scheele.

Heller published Kuhnistera pulcherrima as a nomen novum in 1895 and based it on P. virgatum Scheele. Following the description he speaks of his finding the plant and recognizing its individuality from other purple flowered species and naming it a "n. sp.," the designation that occurs on his widely distributed No. 1857 (3—ISC, 2—SMU, 2—US, 1—NY, 1—MO, 1—OKLA).

Four years later, Heller transferred K. pulcherrima to Petalostemon along with three other species originally placed in Kuhnistera. Later still, Heller made a final transfer of his species to P. pubescens (A. Gray) Heller, listing P. violaceum var. pubescens A. Gray., P. virgatum Scheele, K. pulcherrima Heller and P. pulcherrimum (Heller) Heller, as synonyms. He concluded with this sentence:

> This beautiful species has been burdened with much synonymy mainly by the writer, who may perhaps be pardoned for not earlier understanding the true place of publication of the first available name, when viewed in the light of the preceding article.

Unfortunately Heller's publication appeared one month after the publication by Aven Nelson of P. pubescens (Bot. Gaz. 31:395. 1901, June) and so it too (the Heller name) is a later homonym and the epithet P. pulcherrimum must be accepted.

Petalostemon pulcherrimum is readily recognized by four characteristics: 1) long peduncles, 2) a long tubular calyx with short lobes, 3) a glabrous calyx tube for the ciliate bands on the lateral margins and 4) short bracts. The growth pattern is variable and ranges from decumbent to erect. This variation was first thought to be due to hybridization with P. decumbens, but analysis shows decumbent material clearly to be P. pulcherrimum. Hybridization with P. purpureum has been previously discussed.

Description

Stems many, usually robust, varying from erect to decumbent, 3.5-7.5 dm in length, usually smooth near the base, becoming striate in upper portions; red "glands" apparent on dried stem, 1 mm in diameter, flush with surface; three vertical ribs below leaf axes not obvious on lower parts of stems but becoming obvious above; glabrate to moderately pubescent, usually more pubescent at apex of peduncle. Stipules subulate-setaceous, 3-15 mm in length. Leaves fascicled, seldom more than three trifoliate leaves in axils; leaflets 3-7, the terminal one to 26 mm long and 3 mm at widest point, elliptical, slightly involute; glandular and glabrous above. Peduncles 4-15 cm long. Inflorescence a columnar, nonexpanding spike, 15-35 mm long, 11-14 mm wide. Bracts not precocious, never exceeding calyx lobes even in bud; acumen 0.6-1.2 mm long, subulate, drying black, always shorter than the calyx lobes and usually as short as the tube itself at anthesis; body, 2.5-3.0 mm long,

not markedly expanding distally, pubescence restricted to a transverse belt of appressed cilia immediately below the acumen and a ciliate fringe along the margin toward the rachis, strongly clasping the calyx throughout its length. Calyx tubular, dorso-lateral surfaces flat, ventral surface curved; tube glabrous, white, drying to a pale, thick, parchment-like surface save for two bands of appressed cilia along lateral margins, silvery, drying rufous; entire calyx tissue infiltrated with a gum, which dries to a shiny red, often showing through to the outside as red streaking; tube 3.2-3.9 mm long and 1.9-2.4 mm in diameter; lobes pubescent, especially on margins, incurved and valvate in bud, opening slightly at anthesis, usually flared in fruit, dark green, drying reddish on the outer surface, remaining green on the inner, the ventral lobe 1.0-1.6 mm long; extruded red gum lobelets ca. 0.1 mm long scattered along margins. Corolla blue to lavender-purple, the standard suborbicular and slightly lobed, 2.5-2.9 mm wide, 2.7-2.8 mm long, the claw 4.0-4.5 mm; in fresh flowers the claw is parallel to the staminal tube until just below the blade whence it reflexes upward at 90°; the apical petals oblong, sometimes slightly obovate, 3.1-4.2 mm long, 1.2-1.4 mm wide, the lateral pair with claws offset to one side, in the fresh flower arching up above, and lateral to, the medial pair; claws 1.0-1.4 mm long. Staminal tube exserted beyond the calyx lobes; filaments purple when fresh, anthers bright orange, exceeding the apical petals, the longitudinal dehiscence lines deep red. Ovary completely glabrous, 1.3-1.7 mm long, 0.8-1.2 mm in diameter; style usually completely glabrous, occasionally slightly ciliate dorsally on the proximal third, inserted slightly below the longitudinal axis of the ovary, never exceeding the exsertion of either petals or anthers, pigmented purple distally. Pod developing mostly ventrally and distally, the proximal tissues of the style persisting as a dorsally directed beak.

Distribution and phenology

Restricted to rich, blackland prairies and associated areas in east-central Texas and adjacent counties in southern Oklahoma. Occurrence in western Texas (Hudspeth County) and New Mexico (Socorro County) is documented by only one collection each, possibly representing introductions or errors in collection data. Primary flowering time is from mid-May to early June.

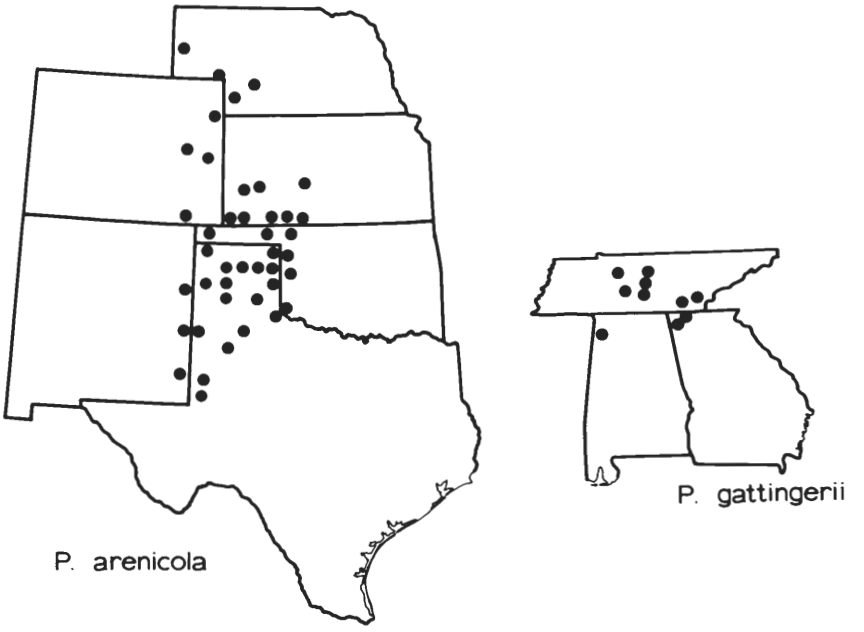
26. PETALOSTEMON DECUMBENS Nutt. (Map 14, Fig. 11B)

Petalostemon decumbens Nutt. Jour. Acad. Nat. Sci. Phil. 7:93. (1834). Type in NY. (1)(2).

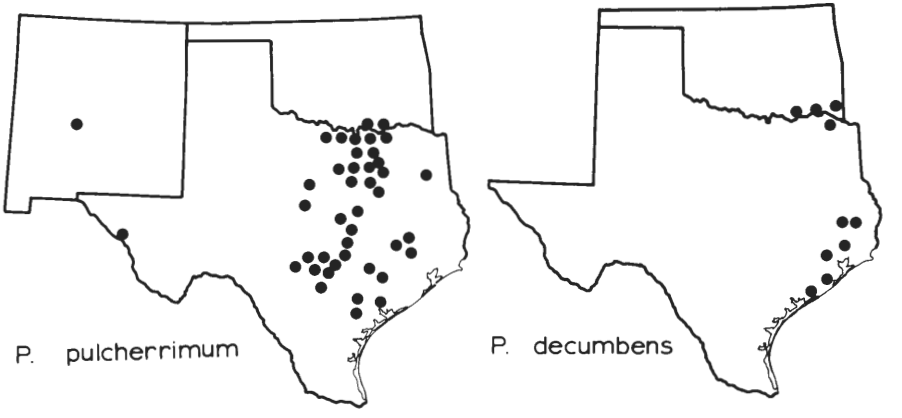
Kuhnistera decumbens (Nutt.) Kuntze. Rev. Gen. Pl. 1:192. (1891). Based on Petalostemon decumbens Nutt.

Nomenclature and observations

Nuttall's definitive description (loc. cit.) concludes, "On the plains of the Red River, Common, Flowering in June." The specimen at Philadelphia is labeled in Nuttall's hand, "Arkansas." Adjacent to the name P. decumbens is an asterisk, Nuttall's designation for a new species. The asterisk, however, is in pencil, not ink, as is the rest of the label. A specimen in the New York type collection is labeled in Nuttall's handwriting with the location, "Red River." It too has an asterisk but in ink



Map 13. Geographic distribution of Petalostemon gattingeri and P. arenicola.



Map 14. Geographic distribution of Petalostemon decumbens and P. pulcherrimum.

of the same type as the rest of the label. It is a better specimen than the one at PH which has lost most of its leaves. A third Nuttall specimen at Cambridge labeled, "Arkansas Red River" lacks an asterisk. Presumably these three sheets were in Nuttall's possession when he prepared his description and were subsequently distributed. It seems best to choose the specimen at NY to be the lectotype on the basis of, 1) the distinguishing asterisk matching the rest of the label, 2) the same locality as in the description, and 3) the quality of the specimen.

The distributional pattern of this species is unique, the two disjunct areas being separated by over 200 miles. The soil types, however, are very much alike, both calcareous in nature. The southeastern counties of Oklahoma possess other restricted species; e.g., Leavenworthia aurea Nutt. and Lesquerella angustifolia (Nutt.) Wats. (Criciferae). Rollins (1956, 1963) attributes the limited range of L. aurea to the thin soil with underlying horizontal limestone strata—a glade condition. This species, also bicentric in its distribution, has been collected in San Augustine County, Texas—within 50 miles of the southern distribution of P. decumbens. It is probable that the habitat dictates the distribution of L. aurea and P. decumbens in the same manner.

Hybridization between P. decumbens and P. purpureum in southeastern Oklahoma has already been discussed.

Description

Stems many, arising from a prominent caudex, usually decumbent and apically ascending, occasionally erect, partially supported by adjacent vegetation, 2-5 dm long, glabrous and smooth at base becoming slightly pubescent and striate above. Stipules 4-6 mm long, subulate, never thicker than 0.5 mm at base. Leaves fascicled with seldom more than 2 trifoliate leaves in axes of major leaves. Leaflets 7-9, elliptical, 17-25 mm long, 3.0-4.6 mm wide, rarely involute, the tip subulate; rachis extended beyond distal pair of leaflets 0.5-3.5 mm. Peduncle short, often lacking, never over 3 cm long. Inflorescence a columnar, non-expanding spike, 14-36 mm long, 13-16 mm wide. Bracts long-acuminate, exceeding the calyx in bud and at anthesis; body 2.8-3.5 mm long, neither strongly clasping nor sharply narrowing at base, lateral margin often scarious; entire bract glabrous save for a small triangular area of appressed cilia at widest part; body gradually tapering distally to a narrowly lanceolate acumen, 4-17 mm long, often reflexing abaxially. Calyx tubular, deltoid in cross-section with a rounded base; tube generally glabrous except for two bands of appressed cilia along lateral margins which traverse the entire length of the calyx and general appressed pubescence between the bands on the proximal 1/3 of the tube; tube 3.6-4.3 mm long, 2.2-2.6 mm in diameter; lobes pubescent, incurved, valvate in bud, barely opening at anthesis, ventral lobe 2.0-2.1 mm long. Corolla blue to blue-purple; standard blade oval-deltoid, strongly concave, not basally lobed, 2.3-2.7 mm wide at base, 2.4-3.0 mm long, the claw 5-6 mm long; apical petals oblong, often slightly lobed at the base, 3.5-4.0 mm long, 1.2-1.5 mm wide, the claw 1.0-1.4 mm. Staminal tube not exserted beyond the calyx lobes; filaments tinged blue-purple, exceeding petals; anthers orange, the dehiscence line bright red. Ovary glabrous, 1.5-1.7 mm long, 0.9-1.1 mm in diameter; style usually glabrous,

occasionally slightly ciliate, roseate at tip, exserted slightly beyond anthers soon after anthesis. Pod developing by enlargement of the ventral-distal portions of the ovary, the style base persisting as a beak on the legume.

Distribution and phenology

Distribution bicentric. Northern populations found in counties of southeastern Oklahoma and adjacent counties in northeastern Texas. Southern population center is in southeastern Texas. Restricted to calcareous soils with underlying horizontal limestone strata—glade conditions. Flowering from mid-April to early June, reaching a maximum in early May.

27. PETALOSTEMON PURPUREUM (Vent.) Rydb. (Map 15, Fig. 11C)

Petalostemon purpureum (Vent.) Rydb. Mem. N.Y. Bot. Gard. 1:238. (1900). Based on Dalea purpurea Vent.

Dalea purpurea Vent. Desc. Pl. Cels. pl. 40. (1800). Type in G. (1)(2).

Dalea violacea Michx. ex Willd. Sp. Pl. III 1337. (1802). Original material in B. (1)(2).

Petalostemon violaceum Michx. Fl. Bor. Am. 2:50. (1803). Original material in P. (1)(2).

Psoralea purpurea Poir. in Lam. Encycl. Meth. 5:694. (1804). Based on Dalea purpurea Vent.

Petalostemon violaceum var. pubescens Gray. (Quoad material in part non citation) Smith. Contr. Knowledge 3:46. (1852). Based on Petalostemon virgatum Scheele.

Kuhnistera purpurea (Vent.) MacMillan. Metas. Minn. Vall. 329. (1892). Based on Dalea purpurea Vent.

Petalostemon molle Rydb. Mem. N.Y. Bot. Gard. 1:238. (1900). Original material at NY. (1)(2).

Petalostemon pubescens A. Nels. Bot. Gaz. 31:395-396. (1901). Holotype in RM. (1)(2). Not P. pubescens (Gray) Heller (1901) which is P. pulcherrimum.

Petalostemon purpureus mollis (Rydb.) A. Nels. New Man. Bot. Cent. Rocky Mts. Coulter and Nels. 299. (1909). Based on Petalostemon mollis Rydb.

Petalostemum purpureum f. arenarium Gates. Torreya 2:125-128. (1911). Holotype at F. (1)(2).

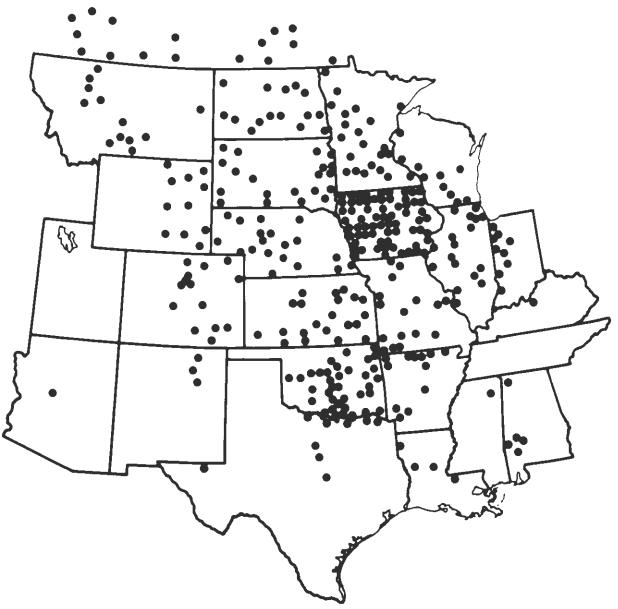
Petalostemon standleyanus Rydb. Fl. N. Am. 24:131. (1919-1920). Type in US. (1)(2).

Petalostemum purpureum f. pubescens (Gray) Fassett. (Quoad concept non basionym) Rhodora 38:96. (1936). Based in part on P. violaceum var. pubescens Gray.

Petalostemum purpureum f. albiflorum Horr. and McGreg. Trans. Kan. Acad. Sci. 55:175. (1952). Holotype at KANU. (1)(2).

Petalostemon purpureum pubescens (A. Nels.) Harr. Manual Pl. Colorado 319. (1954). Based on P. pubescens A. Nels.

Petalostemon purpureum var. pubescens (Gray) Boiv. (Quoad concept non basionym) Nat. Canad. 87:43. (1960). Based on P. violaceum var. pubescens Gray.



Map 15. Geographic distribution of Petalostemon purpureum.

Nomenclature

Petalostemon purpureum was observed and collected by Michaux in Illinois and introduced into Europe in 1794. Verification of this date is given by Ventenat (loc. cit.) and by a label affixed to one sheet of Willdenow's original material at B: "ab Ann. 1794." The Ventenat name appeared in, Description das plantes nouvelles et peu connues, cultivées dans le jardin de S. M. Cels, and he made good use of the unusual opportunity ot studying an American plant growing in European soil. His description and accompanying drawing are superior. His collection is currently housed in the Herbarium Delessert, Conservatoire et Jardin Botaniques, Geneva. In the collection are two specimens, the clearly marked "Dalea N. Sp. purpurea Hort. Cels," the other, "Dalea purpurea Vent. H. C. —violacea W. Petalostemon violaceum Michx." I take the former to be the typus.

The Willdenow collection at Berlin-Dahlem possesses three sheets referable to Willdenow's Dalea violacea that appeared in Volume III of Species Plantarum, the name attributed to Michaux. Michaux' original material is in Paris. Dr. A. Lourteig kindly sent me two specimens representative of the material in the Herbarium Richard. They are both of one species but differ in degree of pubescence, a common variation seen throughout the range of P. purpureum.

The problems involved in typification of Petalostemon violaceum var. pubescens Gray has been discussed under P. pulcherrimum. In summary, Gray's variety is P. pulcherrimum as to citation, but his material included both P. purpureum (Fendler No. 137) and P. pulcherrimum

(Lindheimer No. 42). Both P. purpureum f. pubescens (Gray) Fassett and P. purpureum var. pubescens (Gray) Boiv. are based on the Fendler specimen.

Petalostemon mollis Rydb. is based on four collections. I have seen duplicates of Canby, Snowy Mts., 1882 from Montana at NY. The specimens are very pubescent plants, practically lacking a peduncle, possessing leaflets only slightly involute making them seem quite wide in comparison to other members of the species. In addition, the apical petals are uncommonly wide and represent the measurements in parentheses in the descriptions of these structures. A similar phenotype also occurs in southeastern Colorado but possesses a prostrate-assurgent habit, and has received the name P. pubescens A. Nels. The holotype for the Nelson name is at RM and an isotype at MO. Both of these forms of P. purpureum are apparently rare. I have seen only six sheets including the types which fit the description of P. pubescens and only the two sheets referrable to the Rydberg "species."

Rydberg in his portion of Flora of North America (loc. cit.) created P. standleyanus for the moderately pubescent purple species found in New Mexico. I have studied the holotype, and found it falls within my delimitation of P. purpureum. It most closely resembles the more pubescent forms found in Colorado and Wyoming, particularly regarding petal size and calyx length.

Description

Root black with multiple stems arising from a prominent caudex. Stems usually erect, 2-8 dm tall, ± pubescent, generally branching near the top, striate with three prominent vertical ribs immediately below each leaf. Stipules subulate, glabrous, reaching a maximum of 8 mm, drying dark, often fugacious. Leaves prominently fascicled, each leaf bearing at least two trifoliate leaves in its axil and often an entire compressed branch system; modes usually close together giving the plant a dense, leafy appearance. Leaf rachis extending to 3 cm bearing 3-5 (7) linear, strongly involute leaflets, 6-20 mm long and 0.8-2.0 mm wide; the proximal pair inserted in the distal 1/3 of the rachis; petiolules usually ciliate even in otherwise glabrous material; lower surface, when dried, dotted with small, dark glands and often pubescent, the upper surface nonglandular and glabrous. Peduncle short, usually less than 1/4 the entire height of stem, usually more pubescent above than below. Inflorescence a compressed, nonexpanding, columnar spike, usually at least three times as long as wide, 30-70 mm long, 10-15 mm in diameter. Bracts persistent and precocious, exceeding the calyx in but but usually shorter than the lobes at anthesis; acumen dark, subulate, often pubescent; bract body expanded distally and covered with a characteristic transverse band of appressed cilia, glabrous and contracted proximally, tightly clasping the calyx base, the calyx ± tubular, 2.5-4.0 mm long, not conspicuously ribbed, usually entirely covered with appressed, silvery pubescence; the three lower lobes often incurved toward the calyx axis, the ventro-lateral pair often overlapping the dorso-lateral lobes; the ventral lobe 1-2 mm long, all lobes green tipped, sometimes becoming bald but the margin always ciliate. Corolla varying from pale purple to a deep red-purple, standard globose and concave, often with prominent auricles flanking the claw, the blade 1.4-2.4 mm in diameter, the claw

3.4-4.0 mm; apical petals spreading at anthesis, the blades oblong, 2.5-3.0 mm long, 0.8-1.0 (1.5) mm wide. Staminal tube equaling or exceeding the calyx lobes; filaments tinged purple with the anthers exserted beyond the petals; the pollen orange. Ovary spherical or slightly elliptical, bearded on the distal-ventral half, the dorsal surface bald; style arising on the longitudinal axis of the ovary, bearded proximally and dorsally 1/3 to 1/2 its length, usually exserted beyond the anthers soon after anthesis.

Distribution and phenology

Throughout the short grass plains and prairies of southern Canada and the United States. North to south: from southern Alberta, Saskatchewan and Manitoba, to eastern New Mexico, central Oklahoma and Arkansas; scattered in isolated colonies in Louisiana, Mississippi and Alabama; in Texas along the Red River Valley and rarely into the Black Belt Prairie region. East to west: from central Indiana to Montana, central Wyoming and central Colorado.

Anthesis: northwest, mid-June to early August; southwest, late May to late July; northeast, late May to mid-August; southeast, mid-May to early June.

Observations

Petalostemon purpureum is variable with respect to amount of pubescence. Truly glabrous individuals are rare, but they are found throughout the entire range of the species. Most specimens are pubescent at least on the petiolules and the lower surface of the leaflets. The greatest number of extremely pubescent plants is found in the northwestern part of the range and Colorado to New Mexico. However, glabrate or completely glabrous specimens are not lacking in these areas. For example, A. Hayden, July 1929, Ft. Collins, foothills, is represented by two sheets (ISC 101400, 101735). One specimen is moderately pubescent, the other is glabrous. Close examination of both indicates, however, that in all other respects, the two entities are identical. Collections from Montana indicate that the specimens from higher elevations are generally low in stature but a wide range of pubescence is exhibited. Pubescence variations in the Canadian specimens parallel those found in the United States. Toward the west, there is a greater proportion of pubescent forms, yet in the same areas where the "mollis" forms are found, there are glabrate ones. A collection from the extreme northwestern part of the range in Alberta is almost glabrous [G.H. Turner, 17 (NY)].

Disposition of pubescent, broad-leaved variants—P. pubescens A. Nels. and P. mollis Rydb.—is difficult. From my herbarium study of these taxa, they seem more deserving of some taxonomic rank than any other variation in the extensive P. purpureum complex. Harrington (loc. cit.) relegates P. pubescens A. Nels. to the subspecific level and comments, "Intergrades with the typical form."—a comment presumably based on field experience. Lacking personal field experience in this region, I am adopting a conservative approach and considering the two as phenotypic extremes of an inherent polymorphism in this widespread species. The names are relegated to synonymy.

A cinereous or silvery-pubescent condition of the calyx and rachis is characteristic of P. purpureum. The rachis pubescence is usually

carried to slightly below the inflorescence. The calyx tube is always invested with appressed, to slightly spreading pubescence but "balding" of the lobes occurs spradically throughout the range. It is most common in specimens from Arkansas and Missouri, especially those collected in the vicinity of Kansas City, but it is also found as far north as Wisconsin. This variation accounts for the reports of the occurrence of P. pulcherrimum north of Texas and southern Oklahoma. My studies indicate that this is no evidence for introgression with any other species. Calyx pubescence variation does not seem of sufficient significance to justify nomenclatural recognition.

The growth habit of certain southeastern specimens of P. purpureum is different from that in other parts of the range. Several collections from Arkansas, Louisiana and Alabama are decumbent or prostrate. With this is coupled the possession of extremely small leaves and small flower spikes. In all other respects (i.e., floral characters) these plants cannot be excluded from P. purpureum. They are generally limited to specific habitats, for example, "glades" or chalky-marl soils. The holotype of P. purpureum f. areniarium Gates, a sand dwelling "ecotype" from Illinois possesses many of the same characteristics. Perhaps there has been phenotypic convergence between these widely separated populations since both grow in rather unusual environments for the species.

The normal leaflet number for P. purpureum is 3-5. In the five leaflet form, the proximal pair of leaflets are invariably inserted on the distal one-third of the rachis. Specimens possessing seven leaflets are rare, but scattered throughout the range of the species from such widely disparate locations as Lucas Co., Iowa; El Paso Co., Colorado; and Blaine Co., Oklahoma. Of the over 800 specimens of Petalostemon purpureum I have examined, only ten had seven leaflets.

Hybridization between P. pulcherrimum and P. decumbens and P. purpureum has been discussed previously.

28. PETALOSTEMON TENUE (Coult.) Heller (Map 12, Fig. 11D)

Petalostemon tenue (Coult.) Heller. Bull. Torr. Bot. Club 26:593. (1896). Based on Petalostemon violaceus var. tenuis Coult.

Petalostemon violaceus var. tenuis Coult. Contr. U.S. Nat. Herb. 1:34. (1890). Type in US. (1)(2).

Kuhnistera tenuis (Coult.) Heller. Bull. Torr. Bot. Club 23:124-125. (1896). Based on Petalostemon violaceus var. tenuis Coult.

Petalostemon stanfieldii Small. Fl. S.E.U.S. 631. (1903). Type in NY. (1)(2).

Petalostemon grothii Macbr. Contr. Gray Herb. N.E. 49:49. (1917). Type in GH. (1)(2).

Dalea tenuis (Coult.) Shinners. Field and Lab. 17:84. (1949). Based on Petalostemon violaceus var. tenuis Coult.

Dalea stanfieldii (Small) Shinners. Field and Lab. 17:84-85. (1949). in part. Based on Petalostemon stanfieldii Small.

Dalea purpurea var. tenuis (Coult.) Shinners. Field and Lab. 21:165. (1953). Based on Petalostemon violaceus var. tenuis Coult.

Nomenclature and observations

The primary unifying characteristics of this species are its distribution and habitat preference, and the possession of retrorse pubescence on the calyx tube. The latter character is unique in the genus.

This taxon has been known as P. stanfieldii Small, but it must yield priority to the earlier P. tenue (Coult.) Heller. Both types fall within the circumscription of this species as I understand it. The type specimen of P. violaceum var. tenuis Coult. is in US, No. 23346, Santa Anna, Coleman Co., Texas. G. C. Nealley, 1889. A photograph is also at NY. The Coulter interpretation is not without flaws (loc. cit.). Following a brief description he states:

> Santa Anna (Coleman county). Apparently the form referred to in Pl. Fendl. under No. 138. The species is an exceedingly variable one, but the above variety is so distinct that it seems to deserve a name and a description.1

I have seen Fendler No. 138 (MO), and it is clearly a P. tenuifolium with expanding spikes and spreading pubescence.

In the transfer of Coulter's variety to species level, Heller (loc. cit.) makes this pertinent comment:

> This is a very good species, quite distinct from the Petalostemon violaceus, which has been made a dumping ground of various red-flowered species which are not at all related to it. This species is much more closely related to Reverchoni than to purpurea.

With this I concur.

In his description of Petalostemon stanfieldii, Small does not name a type (loc. cit.), merely listing the distribution as, "On plains or prairies, Texas." There is a specimen in the J. K. Small collection at NY labeled "Type," in what I take to be Small's handwriting. It was collected by S. W. Stanfield, Summer 1896 at San Marcos and vicinity." Rydberg (loc. cit.) apparently accepted this specimen as the type because he indicates, "Type locality: San Marcos, Texas."

The type collection of Petalostemon grothii is at GH. I have also studied an isotype from US, No. 717748. Although collected in fruit, it is without a doubt P. tenue as herein described. MacBride (loc. cit.) comments on the persistence of the bracts (visible only in fruit) which is unique among purple species. The collecting site is within the range of P. tenue, also.

Shinners (loc. cit.) transferred both P. tenue and P. stanfieldii to Dalea. Under that name he included P. pulcherrimum (Heller) Heller and its synonymy. In 1953 he removed P. pulcherrimum and renamed it Dalea helleri Shinners. In the same paper, passing almost unnoticed in the body of the paragraph, is a retraction of his acceptance of Dalea tenuis (Coult.) Shinners, relegating it to a variety of Dalea purpurea. He based the combination on the type specimen at US, which he saw. He states:

> Considerably resembling D. Helleri is D. purpurea Vent. var. tenuis (Coulter) Shinners, comb. nov. . . ., which has the calyx tube pubescent throughout with more or less appressed hairs instead of loose spreading ones as in var. purpurea. D. purpurea var. tenuis is known from Coleman and Taylor counties; . . .

P. tenue is limited in its distribution to the eastern Edwards Plateau, its escarpment and outliers. It possesses many characteristics in common with P. arenicola, but differs sharply from that species in its distribution, habit preference and the unique characteristics of retrorse calyx pubescence. This can best be observed in a dried specimen because when fresh, the trichomes are silvery-transparent and difficult to see. It is particularly apparent at the base of the calyx.

Two other species have ranges that overlap with that of P. tenue. They are P. pulcherrimum and P. purpureum. P. tenue can usually be differentiated visually on the basis of size, being smaller than the other two species both in stature and spike size. It also has a habitat preference decidedly different from that of P. pulcherrimum in that it is found in rocky limestone areas, whereas P. pulcherrimum is characteristically found in black calcareous soils in this region of Texas.

Description

Stems many, branching above, 2.0-5.5 dm tall, pale, moderately striate with three prominent vertical ribs below the nodes, usually glabrous but occasionally evenly glabrate; center stems erect, peripheral ones often almost parallel with the ground. Stipules setaceous, dark, to 4.5 mm in length. Leaves fascicled; nodes close, producing a leafy appearance; leaflets 3-5 (7), the proximal pair inserted in the distal one-third of the rachis, prominently gland-dotted below and often moderately ciliate. Peduncles long, 3-18 cm, from 1/5 to 1/2 total length of the stem, usually glabrous, rarely pubescent immediately below the spike. Inflorescence a compact nonexpanding spike, often conical in bud, becoming columnar in fruit, 12-44 mm long, 7-11 mm in diameter; rachis pubescent; bracts precocious but at anthesis equal to or shorter than the lobes, body 2.4 mm long, the dark acumen 1.3-2.2 mm long, a slight pubescent band at broadest part of bract body (about in the middle of the whole bract), usually with a ridge of cilia along the back toward the rachis; from the transverse belt of cilia proximally, the margin of bract is fringed; base of bract neither clasping the calyx nor sharply tapered; entire bract persistent even after mature fruit falls from rachis. Calyx tube campanulate, 2.0-3.5 mm long and 2.0-2.9 mm in diameter, invested with retrorse hairs, all pointed toward base of calyx; pubescence most strongly developed on the lateral ribs; lobes often bald but with ciliate margins; dorso-lateral lobes large, deltoid, arising from flat surfaces of the tube; ventro-lateral and ventral lobes lanceolate, arising from hemispherically curved surface of the tube; ventral lobe 1-2 mm long; in bud, lobes incurved and valvate, scarcely opening at anthesis. Corolla purple; standard auricled, not emarginate at apex, 2.1 mm long, 2.2 mm wide, broadly deltoid; apical petals 1.1-1.5 mm wide and 2.3-3.6 mm long, auricled at base, the claw 0.5 mm long. Stamens bright orange, extended as far as the petal tips. Ovary glabrous save for a few cilia distally and dorsally in some specimens, never bearded ventrally, 1.1-1.9 mm long, 0.6-1.0 mm in diameter, usually less than twice as long as high; style inserted on the longitudinal ovary axis, bearded dorsally for half its proximal length. Legume ventral surface developing more than dorsal so that in fruit the beak (remnant of style) is offset dorsally.

Distribution and phenology

Limited to the eastern Edwards Plateau in Texas and adjacent areas to the east; north and south from Wise to Bexar county, east and west from Coryell to Irion county, Texas. Always found in rocky, limestone soil. Common along roadsides. Anthesis beginning in early May, reaching a peak in early June, ceasing by early July.

29. PETALOSTEMON ARENICOLA Wemple (Map 13, Figs. 8; 11 I; 12D)

Petalostemon arenicola Wemple sp. nov.
P. tenuifolium authors pro parte
P. purpureum authors pro parte

Description

Petalostemon arenicola Wemple, sp. nov. Caules e basi (raro superne) ramosi glabri vel glabrati 2-4 (5) dm alti striati. Stipulae subulatae fragiles usque 5 mm longae. Folia fasciculata; foliola 3-5 (7) linearia arcte involuta. Pedunculi caules 1/5-1/2 aequantes; spicae compactae non producentes 2-5 cm longae 6-9 mm latae. Bracteae non amplexicaules nec basi constrictae, cum margine apicali ciliato et cum vitta pubescente prominente transversa in parte expansa; acumen atratum sub anthesi calycis lobis brevius. Calyces tubus campanulatus 2.0-2.9 mm longus, lobi 1.0-1.5 mm longi cum pilis appressis raro demum glabrati. Corolla purpurea. Ovarii apex et venter barbati; stylus dorso barbatum per mediam proximam.

Typus, ISC (Wemple 319).

Plants lacking a prominent caudex; tap root long, pale yellow, 2-4 (5) dm tall, spreading, glabrous or glabrate, striate, prominently 3-ribbed below nodes; branching from the base, seldom above. Stipules subulate, drying dark brown, fragile, to 5 mm in length. Leaves fascicled, primary leaves bearing at least two axillary trifoliate leaves; leaflets 3-5 (7) all inserted in the distal 1/3 of the rachis, linear, strongly involute. Peduncles usually long, 1/5-1/2 the stem length, glabrous. Inflorescence a compact, nonexpanding spike 20-50 mm long, 6-9 mm wide; bracts precocious, exceeding the calyx lobes in bud, shorter than lobes in flower; bract body 2.2-2.8 mm long at anthesis, not constricted toward base nor strongly clasping calyx; bearing an appressed, transverse belt of cilia below the dark, brown-black base of the acumen, a ridge of pubescence often extending proximally down the back of the bract; distal edge of the bract fringed-ciliate, cilia often extending out into the acumen; acumen 0.7-1.4 mm long, drying black-brown. Calyx campanulate, 2.0-2.9 mm long, 2.1-2.7 mm in diameter at mouth, bearing appressed, anteriorly directed, evenly distributed pubescence; dorsolateral lobes deltoid and straight, the ventro-lateral and ventral lobes subulate and incurved; ventral lobe 1.0-1.5 mm long, villous-ciliate, seldom balding. Corolla purple, widely opened at anthesis; standard blade 2.2-2.8 mm across at widest point, 1.8-2.0 mm long, strongly auricled, claw 2.2-2.6 mm long; apical petals oblong, 2.4-3.2 mm long, 1.2-1.6 mm wide, the claws 0.7-1.1 mm. Filaments usually exceeding petals in length, anthers yellow-orange; pollen a bright yellow. Ovary

bearded ventrally on distal half, more than twice as long as its diameter (1.2-1.5 mm long, 0.5-0.7 mm in diameter); style arising from above the longitudinal axis of ovary, bearded dorsally on the proximal end to half its length.

Distribution and phenology

Southwestern Nebraska, eastern Colorado, southwestern Kansas, the panhandles of Oklahoma and Texas and eastern New Mexico. Limited to deep sands of the Llano Estacado, on dunes, blowouts and riverbottoms. Flowering in early July in the northernmost part of the range, early June to early July for the southern part. Texas collections of flowers at anthesis have been made as early as May 1, and as late as August 31. Most collections, however, are as previously stated. The exceptions are probably caused by droughts or early rains typical of the unpredictable rainfall in north Texas.

Discussion

This new species is distinctive both in appearance and in habitat preference from the other purple species of Petalostemon growing in the south central United States. Throughout its range, which is almost precisely the geological delimitation of the Llano Estacado (Fenneman 1931), it is found only in the stream beds, which dissect this massive limestone plateau and stream-associated dunes and blowouts. My field studies indicate that it is never found on the caprock nor partially down canyon walls but only in the sand of the river bottoms. In the southern part of its range it is geographically sympatric with P. tenuifolium. Ecologically the two are quite isolated, however, because the latter species is restricted to the caprock, penetrating only part of the way down the valley walls.

The overlapping distribution, and morphological similarity of P. arenicola and P. tenuifolium has resulted in previous confusion; however, the two are distinguishable morphologically as well as ecologically. The typical P. tenuifolium pubescence pattern (the stem base and the apex of the peduncle pubescent) is never found in P. arenicola. The apex of the peduncle is almost always glabrous in the latter species. One of the easiest field recognition features differentiating the two species is that of rachis elongation. As the spike matures, following anthesis, in P. tenuifolium, it elongates, often becoming sinuous. That of P. arenicola never elongates following anthesis. Accompanying spike elongation in P. tenuifolium is loss of the bracts, whereas, the bracts are retained in P. arenicola. The bracts of the latter species are never pubescent over their entire surface, nor are they as wide as those of P. tenuifolium; additionally, they are ciliate along the distal margin. The two species differ to some degree in calyx pubescence. This feature is a difficult key character, but P. tenuifolium has a more spreading calyx pubescence while that of P. arenicola is more appressed. The ovary at anthesis is linear in P. tenuifolium often being three times as long as the diameter, while in P. arenicola it is usually about twice as long as the diameter. The style is axial in P. tenuifolium but decidedly above the longitudinal axis of the ovary in P. arenicola.

Material of P. arenicola has also previously been referred to P. purpureum. The two taxa are quite distinct even though their geographical

ranges slightly overlap. The simplest, yet perhaps the most effective, characteristic to separate the two species is spike width—the width of a spike at anthesis or shortly thereafter, calyx lobe to calyx lobe. P. arenicola has spikes narrower than 10 mm and P. purpureum has spikes wider than 10 mm. It was this differentiation that Turner (1959) utilized to exclude P. purpureum from the panhandle of Texas. Concomitantly, he broadly defined P. tenuifolium to include P. arenicola. P. arenicola seldom exceeds 3.5 dm in stem length, while P. purpureum is taller; in addition, the stems of the latter species are usually branched above resulting in numerous spikes from each major stem, but branching is uncommon in P. arenicola. P. purpureum possesses relatively short peduncles, and P. arenicola has longer peduncles, usually 1/4 the length of the stems. The peduncle apex is glabrous in P. arenicola, while almost always pubescent in P. purpureum. Bract pubescence differs between the two species in that the ciliation often extends rearward of the transverse appressed belt in P. arenicola while the entire proximal area of the bract is glabrous in P. purpureum. In addition, the expanded, distal end of the P. arenicola bract is ciliate giving it a "fringed" appearance. Lastly, the ovary instead of being almost spherical with the style extending from the center of the ovary as in P. purpureum, is elliptical in P. arenicola—at least twice as long as its diameter with the style protruding from the dorsal surface, not the center.

Another species that could be confused with P. arenicola is P. tenue. The two are separated in range by almost 100 miles but are similar in stature and gross appearance. They are readily distinguished by calyx pubescence. On P. tenue the pubescence is always retrorse, that is, pointing rearward toward the axis of the rachis. In P. arenicola the pubescence is oriented in the typical manner, pointing away from the axis of the rachis. A further difference is the glabrous or slightly ciliate ovary of P. tenue while in P. arenicola the ovary is bearded distal-ventrally.

The differentiated characteristics of P. arenicola and the other purple species discussed are summarized in Table 6.

Greenhouse hybridization experiments indicate that P. arenicola and P. tenuifolium are freely compatible. In fact, in attempted crosses, seed set was unusually high and the hybrids themselves while intermediate in all characteristics were fully fertile. Why do the two species not hybridize in nature? They are seldom separated by more than 1/2 mile, one on the valley floor, the other on the mesa, yet I have seen no hybrids in the field or sheets of any putative hybrids in the herbarium. It is possible that the pollinators of the two are different or that the pollinators are localized, either remaining in the valleys or on the mesas. Another possibility is that the hybrids, while growing vigorously in the greenhouse are less well adapted to the available habitats than the parents in nature, and their survival is limited.

Table 6. Character comparisons between P. arenicola, P. tenuifolium, P. purpureum and P. tenue

Character	P. arenicola	P. tenuifolium	P. purpureum	P. tenue
Plant height	<3.5 dm	< 3.5 dm	> 3.5 dm	< 3.5 dm
Branching	below	below	above	below
Vegetative pubescence	glabrous-glabrate	dense below & above	glabrate to pubescent	glabrous-glabrate
Peduncle length	usually long	long	short	long
Spike width	< 1 cm	< 1 cm	> 1 cm	< 1 cm
Spike elongation	none	much	none	none
Bract pubescence	transverse belt + back rib. Ant. ciliate fringe	uniform	transverse belt only	transverse belt + back rib. Ant. ciliate fringe
Calyx pubescence	appressed antrorse uniform	spreading antrorse uniform	appressed antrorse uniform	appressed retrorse "balding"
Ovary shape	2 x long as high	3 x long as high	1-1½ x long as high	1-1½ x long as high
Ovary pubescence	bearded	bearded	bearded	glabrous

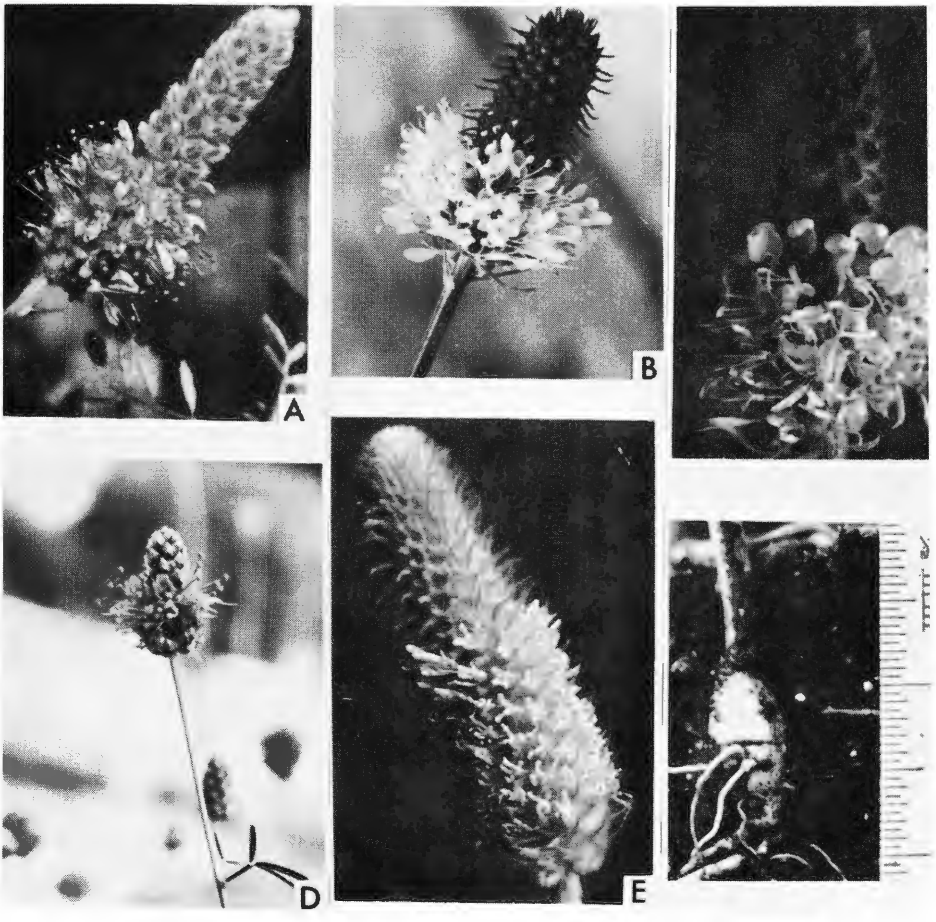


Figure 12. Representative species of Petalostemon (A—E).
The caudex of a seedling of P. candidum (F).
A. P. villosum. B. P. candidum. C. P. microphyllum.
D. P. arenicola. E. P. obovatum.

EXCLUDED SPECIES

Except as indicated, all are annuals referable to Dalea.

Petalostemon confusus Rydb. Fl. N. Am. 24:129. (1919-1920). Type in US. (1)(2).

Petalostemon emarginatum T. and G. Fl. N. Am. 1:311. (1838). Isotype in US. (1)(2).

Petalostemon evanescens (Brandg.) Rose. in Rydb. Fl. N. Am. 24:129-130. (1919-1920). (2).

Petalostemon exile Gray. Pl. Wright. 2:41. (1853). Type in GH; isotype in US. (1)(2).

Petalostemon obreniformis Rydb. Fl. N. Am. 24:130. (1919-1920). Type in US. (1)(2).

Petalostemon oreophilus Cory. Rhodora 41:561-562. (1939). Type in GH; cotype in US. (1)(2).

Petalostemon tripetalus Wils. Kew Bul. 1958:159. (1958). Type in US. (1)(2).

Petalostemon amethystinus Schott. in Wein-Zeitsch. IV. (1830) 1216. ex Endl. in Linnaea VI. (1831). Litt. 55.

This species is perhaps a mislabeled specimen and is currently under investigation by Professor Rupert Barneby (pers. comm. 1966).

Petalostemon chiapense Brandg. Univ. of Calif. Publ. Bot. 10:408. (1924). Type in UC; isotype at US. (1)(2).

Petalostemon pilulosus Rydb. Fl. N. Am. 24:128. (1919-1920).

According to Kearney and Peebles (1960, p. 440): Petalostemon pilosulus (sic) Rydb. was described from a specimen collected by Nealley (No. 237), probably in the Rincon Mountains, Pima County. The type appears to be a form of Dalea albiflora.

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WONIO, MICHAEL LEE
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YORK, DAVID ROSS
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YOUNG, JAMES ANDERSON
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ZIKA, RODNEY GEORGE
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ZIMMERMAN, RICHARD ELMER
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ZYDUCK, THOMAS HERBERT
Numerical Solution of Linear Systems Containing Widely Separated Eigenvalues.
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ABOU-SEADA, MOHAMED SAID
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ADOLPHSON, MARVIN LEE
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BECHNER, JEFFREY PAUL
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BERTRAND, RICHARD DAVID
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BIRZE, ILGA
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KUNDEL, CAROLYN JOY
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KUTLER, PAUL
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LAM, KENNETH MING-CHIH
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LARSON, JON THORSTEN
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